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PALAEONTOLOGY

VOLUME 3 · PART 3

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CORRIGENDA

for *Palaeontology*, Volume 3, Part 3, at Reprinting 1968

page 388, Text-figure caption,
End of first line: For 'teeth or' read 'teeth of'.
End of fourth line: For 'ridge) of', read 'ridge) or'.

page 392, line 14: For 'Position', read 'Posterior'.

CORRIGENDUM

for *Palaeontology*, Volume 3, Part 4, at Reprinting 1968

page 497, Table 1, Column 8:
For 'Hopton Wood Clay', read 'Horton Wood Clay'.

ADDENDUM

page 590, line 3 up: The name *Brightonia* is preoccupied (see Note in Volume 4, Part 2, page 312).

HE MEDIAN ABDOMINAL APPENDAGE OF THE LURIAN EURYPTERID *SLIMONIA ACUMINATA* (SALTER)

by CHARLES D. WATERSTON

TRACT. The results of a study of a series of specimens exhibiting the median abdominal appendage of
nonia acuminata (Salter) from the Upper Silurian of Logan Water, Lesmahagow, Lanarkshire, are given.
anatomy of the opercular appendage of both sexes is redescribed in the light of knowledge obtained from
nt work on related structures in other eurypterids, and the segmented nature of the appendages demon-
ted. Stages in the development of the appendage in both sexes in ontogeny are described for the first time.

INTRODUCTION

XUAL dimorphism was first noted in eurypterids by Woodward (1866–78, p. 61) who
cribed two forms of median abdominal appendage in *Pterygotus bilobus* Salter. Later
the same work, Woodward (pp. 114–19) gave a description of both types of sexual
pendage in *Slimonia acuminata* (Salter) and compared them with the opercular struc-
es of *Limulus*. Since the appearance of Woodward's monograph, much detailed re-
rch has been done on eurypterid anatomy in Europe and America and important
rks dealing with the form of the median appendage and its function have been
lished. An historical summary of earlier work has been given by Størmer (1934*a*,
43–50) who later published two masterly descriptions of the opercular appendages
German Lower Devonian eurypterids: *Grossopteris overathi* (Gross) (1934*b*, pp.
–90) and *Pterygotus rhenaniae* Jaekel (1936, pp. 14–23). Recent detailed descriptions
American eurypterids, in which particular attention is given to the sexual appendage,
lude Kjellesvig-Waering (1948, pp. 22–23) on the Carboniferous *Adelophthalmus*
zonensis (Meek and Worthen), and Caster and Kjellesvig-Waering (1956, pp. 22–27)
the Upper Silurian form *Dolichopterus jewetti* Caster and Kjellesvig-Waering.

The purpose of the present work is to re-examine the opercular structures of *Slimonia*
minata in the light of our greatly increased knowledge of related structures in other
ypterids, and to describe the growth stages of the median appendage of both sexes,
aspect which appears to have received little attention from previous workers. The
dy has been made possible by the large size of the appendages in *Slimonia* which are
en excellently preserved in the Upper Silurian mudstones of Logan Water, Lesmaha-
v, Lanarkshire, from which locality all the specimens examined have come. The
tively large number of available specimens having the opercular appendage preserved
also facilitated the work.

tory of previous work. Neither in Salter's original description of the species (1856,
9) nor in Page's original figure of the genus (1856, p. 135, fig. 3) is the form of the
dian appendage of *Slimonia acuminata* recorded. Huxley and Salter (1859, pp. 59, 60),
vever, figured both types of genital appendage. The type A appendage, using Størmer's

eontology, Vol. 3, Part 3, 1960, pp. 245–59, pls. 42–43.]

classification (1934*a*, p. 46), was regarded as a portion of the epistoma of a specie referred with hesitation to '*Pterygotus*' *acuminatus*, and the type B appendage wa regarded as the epistoma of that species.

The sexual significance of the central lobe of the operculum was first realized b H. Woodward (1866–79, pp. 114–20) who figured both types of appendage and com pared them with the opercular structures of *Limulus*. Unfortunately the supposed sexua dimorphism which he recognized in *Limulus* was based on two distinct species (Pococ 1902, p. 259, footnote). Woodward regarded the tricuspid type A appendage as bein female and the type B appendage as male, and in both he figured what he regarded a genital openings on the deltoidal plates of the operculum. (For definitions of parts se text-figs. 1, 3.) Sutures were not noted in the type A appendage, but in the type B form Woodward described the transverse furrows which occur at the distal end of the append age and which he thought were variable in number and were due to there being a numbe of similar appendages lying one on top of another, the end of each projecting beyon that of the one above it. Laurie (1893, pp. 512–15) adds little to Woodward's descriptio of the type A appendage, except to refute the idea that *Parka decipiens*, sometimes foun in association with it, represents egg-capsules, a supposition which had been used b Slimon and Woodward to support their claim that the type A form was female. Lauri gave a careful account of the type B appendage which he regarded as being a singl structure, the distal end of which was eversible. The variation in the number of furrow a fact which Laurie did not question, he regarded as being due to the different extent t which it was protruded in different cases. In neither appendage did Laurie mention th genital openings described by Woodward, and their existence was queried by Clark and Ruedemann (1912, p. 64), who quoted the findings of Woodward and Laurie an adopted the sex determination given by Woodward. In describing the type B appendage they stated that there are two transverse furrows at the distal end.

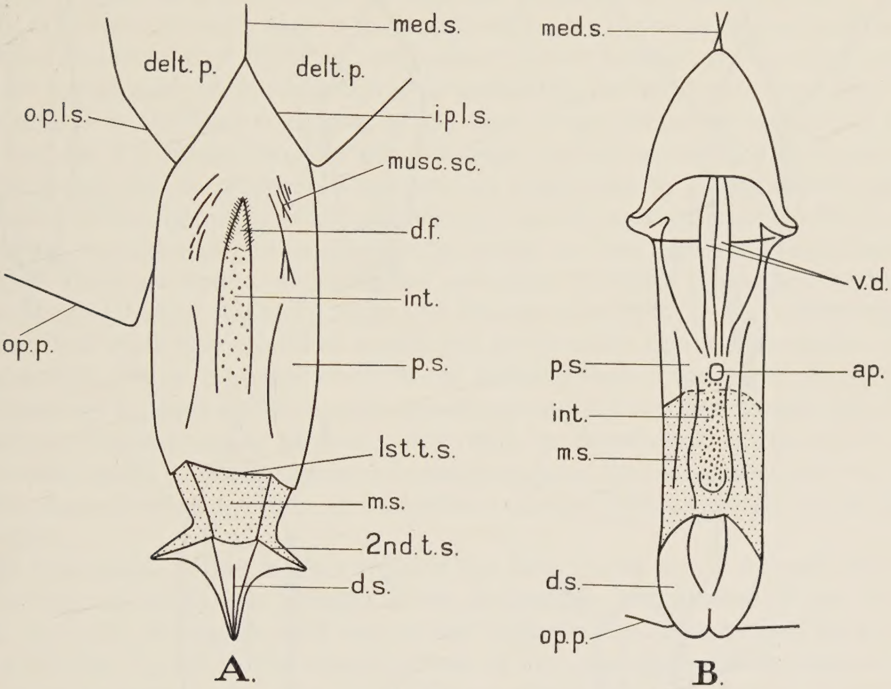
Gaskell (1908) had compared the opercular appendages of eurypterids with those o living members of the Arachnida, and concluded that the type A appendage of *Eurypteri* belonged to the male, and not the female, as had been previously supposed. Størme (1934*a*) found the occurrence of secondary sexual characters in eurypterids, such a clasping organs, to support Gaskell's sex determination, and figured the two types o genital appendage of *Slimonia* accordingly. Through a knowledge of the position o transverse sutures in the type A appendage of other eurypterids, Størmer indicate sutures in his drawing of the tricuspid appendage of *Slimonia*, although these are no repeated in his later figure (1955, fig. 21, 2*c*).

In a paper concerned primarily with the gill-like structures of eurypterids, P. I Moore (1941, p. 66) figured a type A appendage of *Slimonia acuminata* in which tw pairs of ridged areas, interpreted as muscle scars, are indicated near the base of th appendage. Moore did not indicate the presence of transverse sutures on the specime which he figured.

THE TYPE A APPENDAGE

Anatomy of the adult appendage. The appendage is situated behind the paired deltoid plates (delt.p., text-fig. 1) of the operculum. The anterior part of the appendage hastate, the hastation being bounded anteriorly by the inner post-lateral sutures (i.p.l.s of the deltoidal plates. The sutures meet at the anterior tip of the median appendage an ntinue anteriorly as a single median suture (med.s.), separating the paired deltoidal ates, to the anterior margin of the operculum. The deltoidal plates meet the opercular ates (op.p.) in the outer post-lateral sutures (o.p.l.s.) which may be straight or angled using the deltoidal plates to be four- or five-sided.

The shape of the type A appendage is broadly fusiform, the point of greatest breadth ing approximately level with the posterior margins of the opercular plates. The length

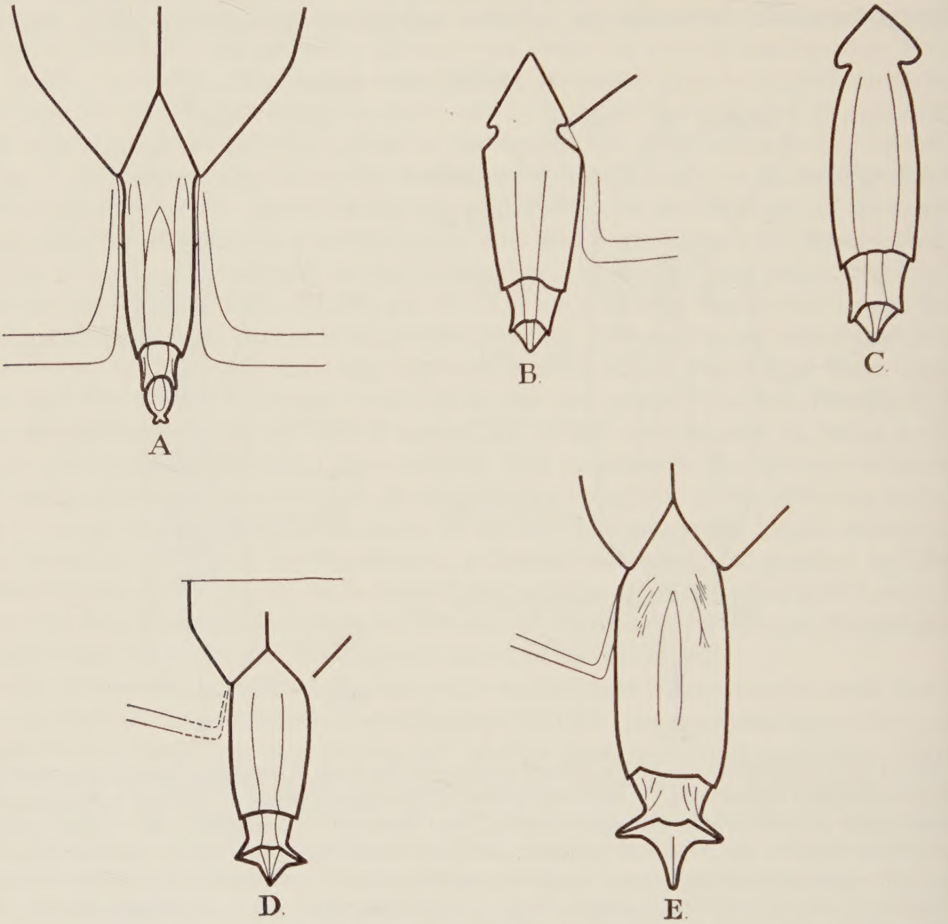


T-FIG. 1. A, Reconstruction of the dorsal surface of the type A median abdominal appendage of *nonia acuminata* (Salter) $\times \frac{3}{4}$. B, Reconstruction of the dorsal surface of the type A median abdomi- appendage of *Pterygotus rhenaniae* Jaekel, after Størmer, ×2 approx. ap. = male gonopore, = dorsal furrow, d.s. = distal segment, delt.p. = deltoidal plate, i.p.l.s. = inner post-lateral ure, int. = thin integument, m.s. = middle segment, med.s. = median suture, musc.sc. = muscle r, o.p.l.s. = outer post-lateral suture, op.p. = opercular plate, p.s. = proximal segment, v.d. = dian canals or *vasa deferentia*?, 1st.t.s. = first transverse suture, 2nd.t.s. = second transverse suture.

between three and four times the breadth. The anterior part of the appendage is state, the posterior portion is trispinate. The posterior spine is normally slightly ger and more acute than the paired spines which extend farther laterally than the atest breadth of the appendage. A marked feature is the asymmetry of the paired nes, one being more posteriorly directed than the other, which is set slightly angled wards the posterior from the normal of the long axis of the appendage.

A longitudinal median ridge extends posteriorly from the rear of the hastate portion the appendage. The margins closely follow the outline of the appendage and taper to arrow keel in the posterior median spine. The median ridge occupies about one-third the width of the appendage.

The type A appendage is divided into three segments by two transverse sutures. The first separates the proximal segment from the middle segment, the former making up least two-thirds of the total length of the adult appendage. The form of the suture vari throughout ontogeny (see text-fig. 2), but in adult specimens it is divided into thr parts. The median section is curved as the suture passes over the median ridge, whi



TEXT-FIG. 2. Growth stages of the type A median abdominal appendage of *Slimonia acuminata* (Salte A, Kelvingrove Museum .09. 123. aa, ×2. B, Kelvingrove Museum .09. 123. aca, ×1. C, Geologi Survey Museum 87280, ×1. D, British Museum (Natural History) 45157, ×½. E, Royal Scottish Museu 1859. 35. 5, ×½.

is wide at this point since the edges of the ridge flare outwards as the posterior marg of the proximal segment is approached. The two lateral sections of the suture also cur outwards as they are traced posteriorly to the margins of the appendage. The form the suture appears to vary in different specimens owing to the accident of flattening the median ridge during preservation. The second suture separates the middle segme from the distal segment. It also has a median curved portion passing over the medi ridge, which again broadens as it approaches the posterior margin of the middle se ment. The lateral parts of the suture pass outwards to the tips of the lateral spines in straight line bisecting them into unequal portions. The part of the spine formed by the middle segment is narrower than the posterior portion formed by the distal segment.

Størmer (1934*a*, text-fig. 19) indicated possible positions for the transverse sutures of the type A appendage, basing his figure on an illustration given by Woodward (1866–78, pl. 17, fig. 2). Examination of this specimen (B.M.N.H. 45157) shows a crack running across the appendage almost midway down the proximal segment which was shown in Woodward's figure and interpreted by Størmer as a suture. The position of the first suture is, however, correctly shown in Woodward's illustration in the more distal position, while the central part of the second suture is drawn between the lateral spines. The sutures are particularly well seen in specimens exhibiting the dorsal side of the appendage.

With regard to the finer structures of the type A appendage, Woodward (1866–78, p. 116, text-fig. 35) figured two circular openings, one on each of the deltoidal plates, which he interpreted as ovipores. These are not mentioned by Laurie (1893) and a re-examination of the figured specimen (B.M.N.H. 44445) does not support Woodward's claim. What were thought of as gonopores appear as two very small wrinkles in the integumen which are neither rounded nor pore-like. It is true that other workers, for example Holm (1898, p. 43) and Clarke and Ruedemann (1912, p. 66 and text-fig. 122), have described what they regard as gonopores as occurring in a rather similar position in other genera. These, however, occur at the lateral points of the hastate basal portion of the proximal segment of the median appendage and not on the deltoidal plates. They are thus not homologous to the pores described by Woodward. In the course of the present study many perfectly preserved specimens have been examined and no similar structures have been seen. They are therefore regarded here as merely an accident of preservation.

In the description of the median ridge it has been stated that it extends posteriorly from the rear of the hastate portion of the appendage. Preparation of one specimen (R.S.M. 1859. 35. 5) suggests that the median ridge may be accompanied by a complementary median furrow in the dorsal surface of the appendage, the opening of which does not extend as far as the ridge itself. The specimen displays a mould of the interior of the dorsal surface of the appendage, and the median ridge was broken away at the midline of the proximal segment rather less than half-way from the anterior tip of the segment. Where the ridge was broken away, two natural margins were revealed converging anteriorly, where they meet to form the boundaries of a lanceolate groove. Hair-like thickenings of the integumen occur along these margins, the hairs being directed posteriorly and diagonally inwards towards the mid-line. The hairs appear to extend beyond the margins and protrude into the groove.

The ridged areas regarded by Moore (1941) as muscle scars flank the median ridge on the proximal segment posterior to the hastation. On Moore's specimen (Sedgwick Museum A 16236) two pairs of ridged areas are seen, the larger being anterior to the smaller, which has a more central position on the appendage (see Pl. 42, fig. 2). Similar areas may be seen in the Geological Survey Nos. 87282, 87283, and 87285; in the Royal Scottish Museum 1859. 35. 5; and in part in the Kelvingrove Museum .09. 123. pi. The areas are marked by narrow branching ridges radiating in a post-lateral direction with intervening smaller, parallel ridges which may be very numerous (see Pl. 42, fig. 3). An examination of the muscular attachments on the dorsal surface of the operculum of *Limulus* has confirmed, in the writer's opinion, Moore's view that the areas represent muscular attachments. The pattern of the markings compares closely with that of the attachment of the 'branchial muscles' in *Limulus* (Benham 1885), although the muscles of the type A appendage of *Slimonia* cannot be regarded as homologous with these.

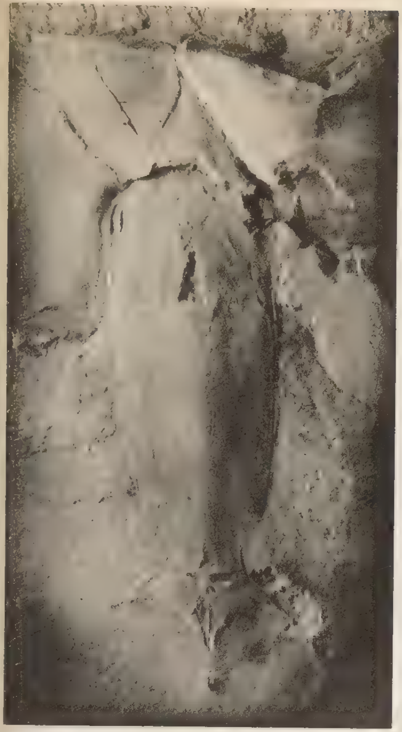
Development of the type A appendage. Examination of a series of type A appendages has shown how different growth stages, exhibiting very different shapes, are related to one another. It has thus been possible to work back from the known adult appendage to the previously unrecognized nepeonic and juvenile forms.

The smallest type A appendage seen has a total length of 24·0 mm. and a maximum breadth of 6·0 mm. and is preserved in the Slimon collection of the Kelvingrove museum No. .09. 123. aa. (see text-fig. 2A, and Pl. 42, figs. 4–6). The maximum width of the appendage is at the posterior angles of the hastation, from which it tapers posteriorly. The proximal segment comprises over three-quarters of the total length of the appendage, as compared with two-thirds in adult examples, and its posterior margin, marked by the first suture, is anterior to the rear margins of the opercular plates. The latter feature has been noted in a nepeonic example of the type A appendage of *Eurypterus fischeri* Eich. by Holm (1898, p. 43, pl. 1, fig. 11). The suture is curved, the convexity towards the anterior, and the post-lateral angles are acute. Lateral spines are not developed, the middle segment tapering towards the posterior, where the post-lateral angles are more acute than in the proximal segment and are posteriorly directed. The second suture, like the first, is curved with the convexity towards the anterior. The distal segment is elliptical, being longer than it is broad, and divides into two minute points at the posterior extremity of the appendage. The median ridge extends from the rear of the hastation to the distal segment, where it terminates before reaching the posterior margin. The opercular plates of this specimen are interesting in that they indicate the transverse fused suture extending laterally from the posterior points of the deltoidal plates, a feature which is rarely seen in *Slimonia* (Pl. 42, fig. 4).

The next growth stage is shown in the Kelvingrove Museum specimen No. .09. 123. aca., in which the length of the appendage is 39·0 mm. and the maximum breadth 14·0 mm. The broadest part lies in the proximal segment behind the hastation. The proximal segment still constitutes about three-quarters of the total length of the appendage. The first suture, however, lies posterior to the rear margins of the opercular plates (see text-fig. 2B). In the post-lateral angles of neither the proximal nor the middle segment is the angle so acute as in the smallest form, although they are still posteriorly directed. The middle segment at this stage is proportionately longer in relation to the other segments than in any other stage in ontogeny, comprising about one-sixth of the total length of the appendage as compared with one-ninth in the smallest specimen. The distal segment is triangular, tapering posteriorly to a point, showing no indication of the small paired

EXPLANATION OF PLATE 42

Figs. 1–6. *Slimonia acuminata* (Salter). Median abdominal appendage Type A. 1, Entire appendage. ×¾, R.S.M. 1859.35.5. 2, Entire nepeonic appendage. ×3, Kelvingrove .09.123.aa. 3, Distal part of the nepeonic appendage showing the distal, middle and part of the proximal segments. Alcohol immersed ×6, Kelvingrove .09.123.aa. 4, Diagrammatic representation of fig. 3. 5, Part of the proximal segment to show the two pairs of muscle scars. ×1½, Sedgw. Mus. A16236. 6, Part of the proximal segment to show muscle scars. ×1½, R.S.M. 1859.35.5.



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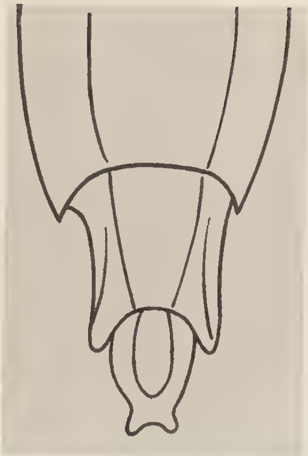

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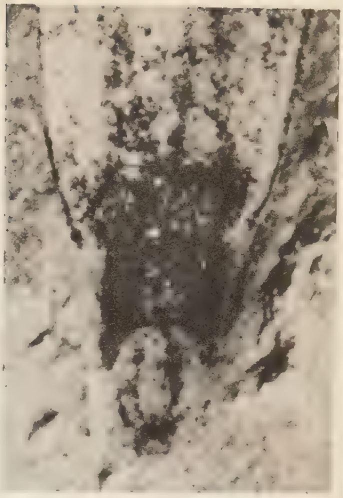

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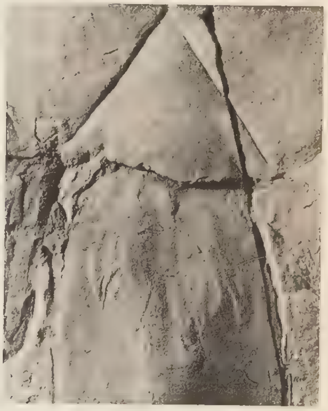

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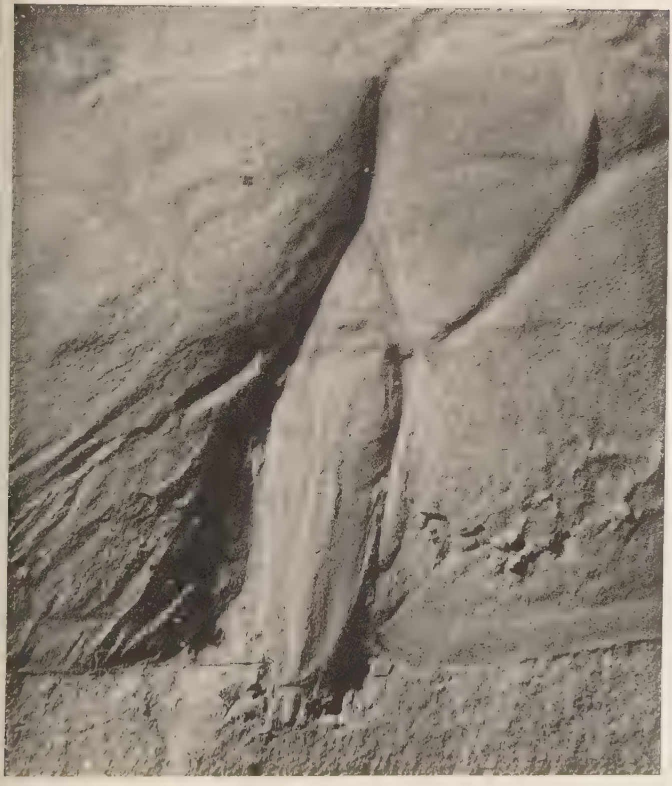

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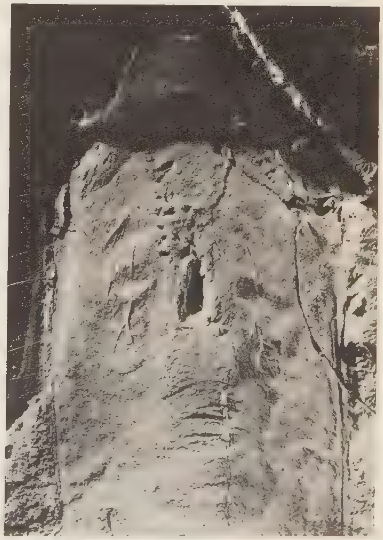

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horns noted at the posterior extremity of the smallest specimen. The length of the distal segment is smaller than the maximum breadth.

An appendage exhibiting a slightly later stage in development is Geological Survey 87280, counterpart 87281, which is probably the specimen which was figured by Huxley and Salter (1859, pl. 15, fig. 3) as a problematical fragment. The length is 48·0 mm. and the maximum breadth 13·0 mm., but the point of maximum breadth lies midway down the length of the proximal segment instead of at its anterior as in smaller examples (text-fig. 2C). In other respects this specimen resembles No. .09.123 aca., except that the median ridge is more pronounced, and as a consequence the sutures have become divided into a central and lateral parts such as is seen in the more adult specimens. The relationship of the first suture with the posterior margins of the opercular plates is not seen, since the appendage has become separated from the rest of the operculum.

The British Museum specimen B.M. (N.H.) 45157 is small but exhibits adult characters (text-fig. 2D). The posterior margins of the opercular plates are now level with the mid-point of the length of the proximal segment. The trispinate distal feature is present although not fully developed. The post-lateral angles of the middle segment have been produced to form the anterior portion of the lateral spines. The antero-lateral parts of the distal segment have also been expanded to form the posterior portions of the lateral spines, angles being developed in the lateral margins of the distal segment between the lateral spines and the posterior median spine. All three spines are less acute than in adult specimens, in which they are still further produced (text-fig. 2E).

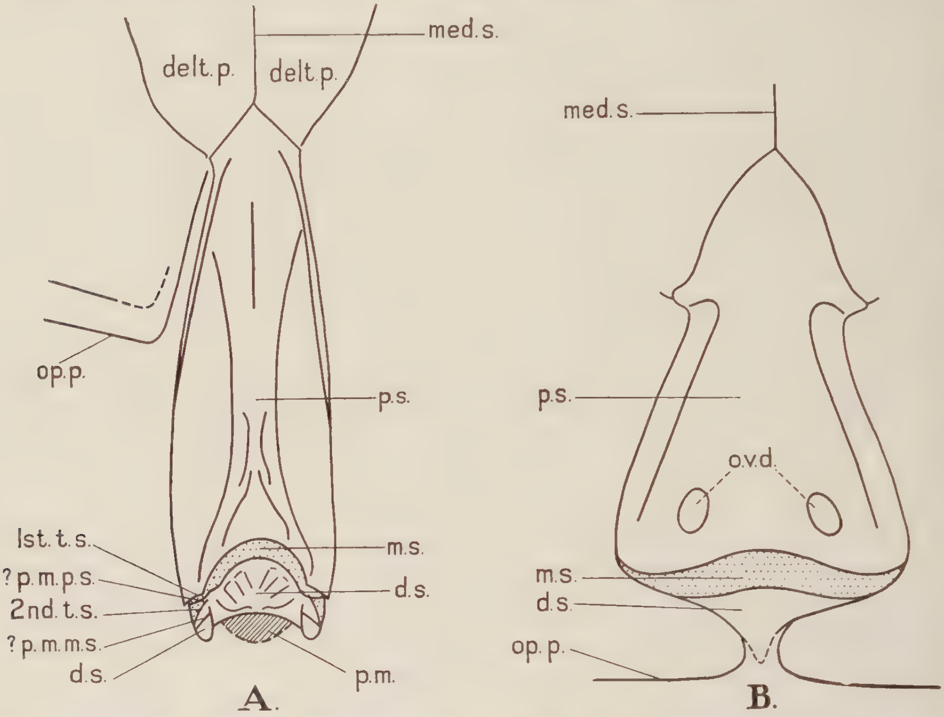
In summary, the development of the type A appendage appears to exhibit the following features:

1. A greater growth rate in the length of the proximal segment in relation to the length of the opercular plates from the condition seen in the nepeonic form, in which the proximal segment does not extend beyond the posterior margins of the opercular plates, to the adult condition in which the rear margins of the opercular plates are approximately on a level with the mid-line of the proximal segment.
2. The gradual posterior migration of the point of maximum breadth in the proximal segment from the anterior part of the segment to half-way down the length.
3. The reorientation of the post-lateral angles of the middle segment from a posterior to a postero-lateral or lateral direction, with their elongation to form the anterior parts of the lateral spines.
4. The changing shape of the distal segment from elliptical to triangular, and finally to the expansion of the antero-lateral parts to form the posterior portions of the lateral spines, and the production of the posterior tip to form the median spine.
5. The early loss of the paired horns at the posterior of the nepeonic appendage.
6. The growth of the median ridge with the consequent change in shape of the sutures from a simple curve to central and lateral parts.

THE TYPE B APPENDAGE

Anatomy of the adult appendage. Relationships between the deltoidal plates, the opercular plates, and the hastate anterior part of the median appendage are the same as those in the type A appendage.

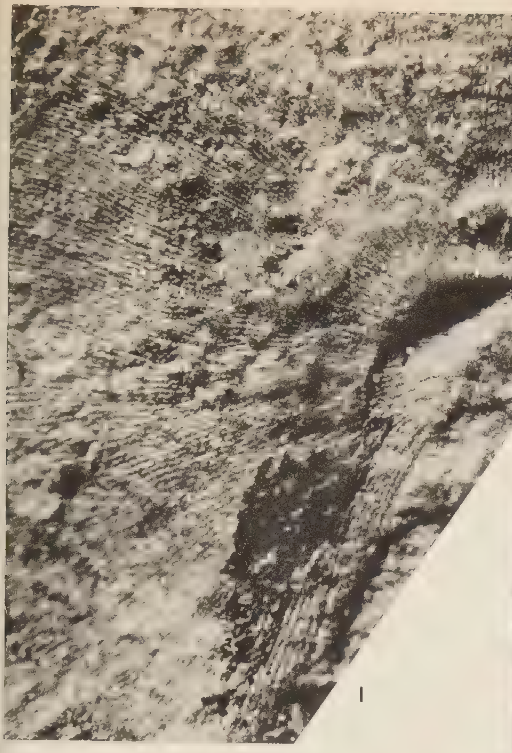
The shape of the type B appendage is fairly narrow and conical, the point of greatest breadth approaching the posterior. It is made up of three segments of which the proximal is by far the largest, comprising approximately eight-ninths of the whole. A median ridge extends across the proximal segment from the lateral points of the hastation to the first suture. The ridge is waisted towards the centre of the segment, but flares out laterally in an ogee curve towards the rear of the segment, and occupies over two-thirds of the width of the segment at the posterior margin. In the Royal Scottish Museum specimen 1859. 35. 7 longitudinal folds of the integumen commence within the median ridge at the posterior third of the proximal segment, and after running parallel for a short distance in the mid-line, curve outwards towards the post-lateral extremities of the median ridge in a more accentuated ogee curve than that followed by the margin of the ridge. This gives the appearance of two ducts or channels passing downwards and out-



TEXT-FIG. 3. A, Reconstruction of the dorsal surface of the type B median abdominal appendage of *Slimonia acuminata* (Salter), ×¾. B, Reconstruction of the dorsal surface of the Type B median abdominal appendage of *Pterygotus rhenaniae* Jaekel, ×2 approx. d.s. = distal segment, delt.p. = deltoidal plate, m.s. = middle segment, med.s. = median suture, o.v.d. = female gonopores, op.p. = opercular plates, ? p.m.p.s. = ? posterior margin of the proximal segment, ? p.m.m.s. = ? posterior margin of the middle segment, p.s. = proximal segment, 1st.t.s. = first transverse suture, 2nd.t.s. = second transverse suture.

EXPLANATION OF PLATE 43

Figs. 1–6. *Slimonia acuminata* (Salter). Median abdominal appendage Type B. 1, Invagination of the right side of the distal segment of the nepeonic form showing the striate ornament. ×144, Kelvingrove .09.123.aav. 2, Distal part of the adult appendage showing part of the proximal, the middle, and the distal segments with post-lateral complexes, note radial fold pattern in integumen of distal segment. ×1½, R.S.M. 1859.35.7. 3, Distal part of a flattened adult appendage showing part of the proximal, the middle, and distal segments with post-lateral complexes, note radial fold pattern in integumen of distal segment. ×1½, Geol. Surv. Scot. 6643. 4, The entire adult appendage, ×¾, R.S.M. 1859.35.7. 5, Distal part of the juvenile form showing part of the proximal segment, the middle segment, and the distal segment with lateral spurs. ×3, Kelvingrove .09.123.vq. 6, Entire appendage of the nepeonic form. ×3, Kelvingrove .09.123.aav.



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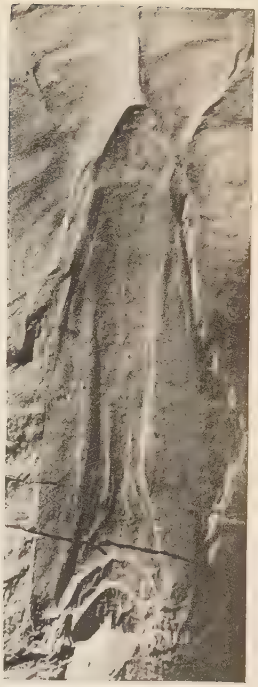

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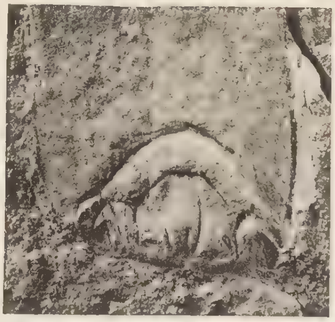

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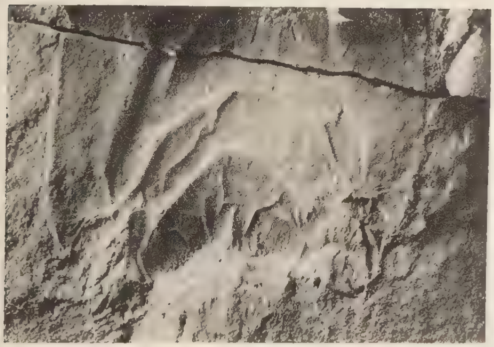

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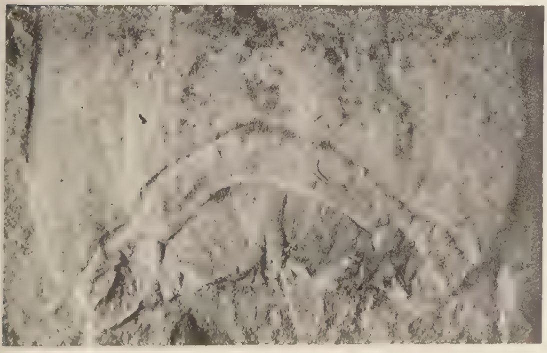

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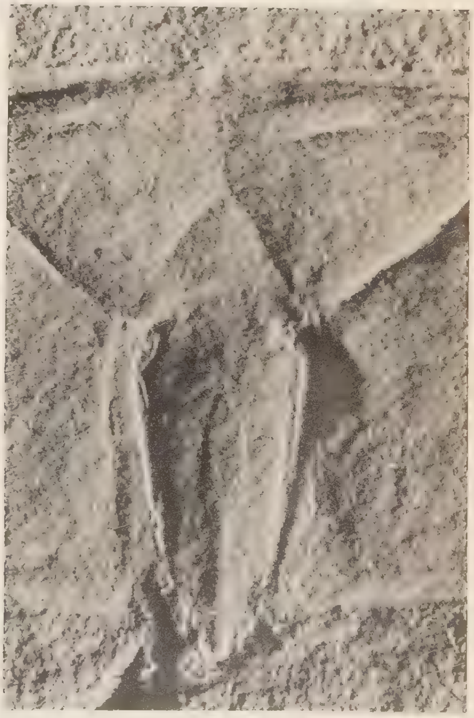

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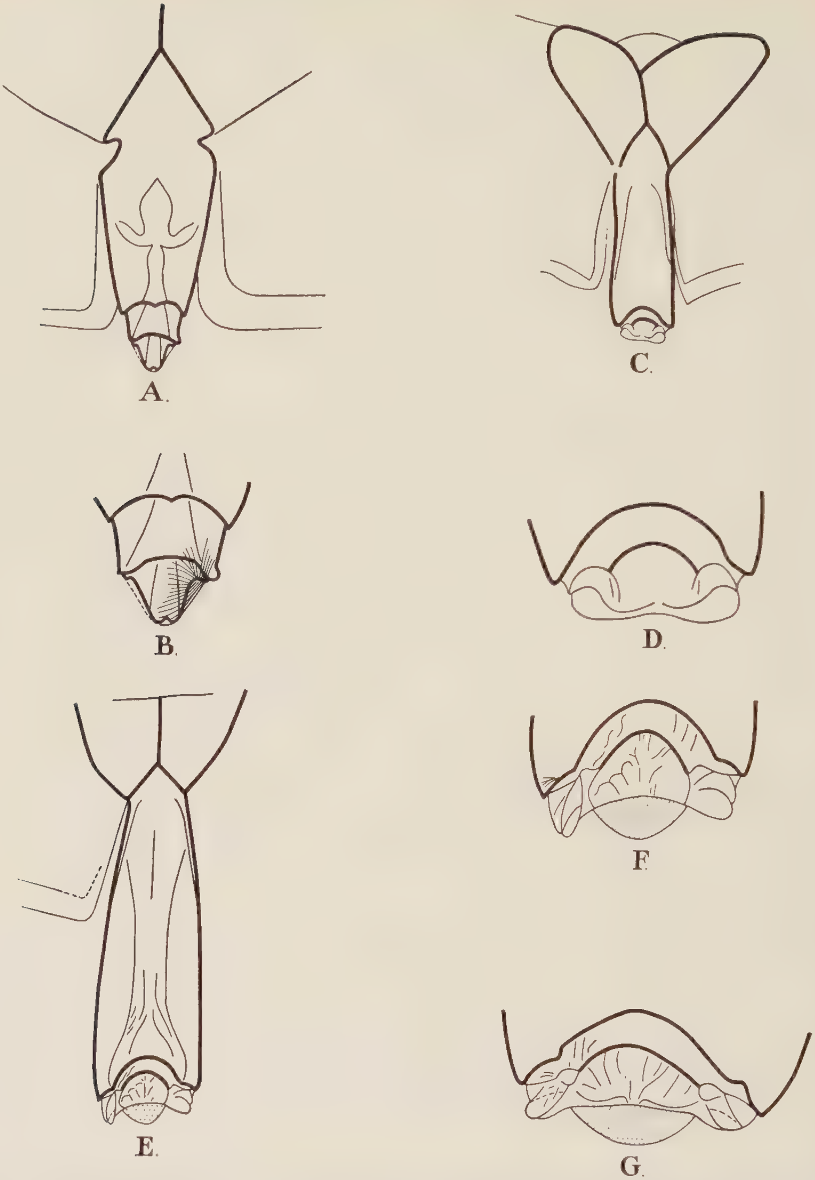
wards to the post-lateral points of the median ridge (see text-fig. 4E, and Pl. 43, fig. 5). The first suture is semicircular in the area of the median ridge, with the convexity towards the anterior. The lateral parts of the suture curve outwards to the post-lateral angles of the proximal segment in shallower curves the convexities of which are also directed anteriorly. The centre part of the second suture is also semicircular, and concentric to the first, thus confining the median portion of the middle segment to a narrow semicircular band. The central part of the distal segment has the form of a half-circle, being bounded anteriorly by the curved second suture, whereas the posterior margin is almost straight. Paired sigmoidal ridges extend laterally from the centre of the segment, near the posterior margin, to join the post-lateral complexes of the appendage.

Previous authors have described the type B appendage as terminating distally in a more or less truncated cone, which is marked by two or three deep furrows (Laurie 1893, p. 513). Laurie advances a convincing argument for refuting Woodward's idea that the type B appendage consists of three similarly shaped median plates, lying one on top of another, the end of each projecting a little beyond the one above, and correctly interprets the transverse furrows as structures belonging to a single median appendage. In addition to claiming that there may be two or three such furrows, Laurie says that the preservation of markings on the remains of these animals seemed to him to depend so much on the details of fossilization, and perhaps also on the condition of the animal at death, and that their presence on some specimens, and absence on others, is not of much weight as an argument. The writer sympathizes with this view since there is a great deal of variation in the appearance of the distal structures of the type B appendage due to the accidents of fossilization, and particularly to the flattening of a three dimensional structure. Careful examination of many adult specimens, however, makes it clear that throughout the variation there can be traced constant features which are due to the original form of the appendage and not to accident. Of these, the presence of two transverse sutures is one constant feature, and the occurrence of what are here termed the post-lateral complexes is another.

The form of the median portions of the two transverse sutures, or furrows, which divide the appendage into proximal, middle, and distal segments has been described. Posterior to the appendage, however, there occurs in some specimens (e.g. R.S.M. 1859. 35. 7 and Geol. Surv. Scot. 6643) a semicircular piece of integumen which probably served to attach the distal part of the appendage to the abdomen of the animal (see text-fig. 4E, F, G). The furrows which exist between the integumen and the posterior margin of the distal segment is probably what Laurie regarded as the third furrow, but is not a true suture.

The post-lateral complexes occur in all specimens which have been examined and are made up of structures developed from the lateral parts of the middle and distal segments. The complexes occur in the post-lateral angles of the appendage. Since their anatomy is more easily understood when their development through ontogeny is known, the description of these features is included in the following account of the development of the type B appendage.

Development of the type B appendage. A small appendage exhibiting the dorsal surface, which is here identified as a type B appendage in the nepeonic condition, is in the Slimon Collection, Kelvingrove Museum No. .09. 123 aav. (text-fig. 4A; Pl. 43, figs. 1, 2). Its



TEXT-FIG. 4. Growth stages of the Type B median abdominal appendage of *Slimonia acuminata* (Salter). A, Kelvingrove Museum .09. 123. aav, ×2. B, Distal portion of Kelvingrove Museum .09. 123. aav, ×4. C, Kelvingrove Museum .09. 123. vx, ×1. D, Distal portion of Kelvingrove Museum .09. 123. vx, ×4. E, Royal Scottish Museum 1859. 35. 7, ×½. F, Distal end of Royal Scottish Museum 1859. 35. 7, ×1. G, Geological Survey Scotland 6643, distal end ×1.

total length is 22·0 mm. and the maximum breadth, which occurs just posterior to the hastation, is 8·0 mm. Behind the hastation the form of the appendage is obconical. The proximal segment does not extend beyond the posterior margins of the opercular plates, and the bounding first suture is arcuate in form. The middle segment is broadest at the anterior and tapers posteriorly, but flares slightly at the post-lateral angles. The second suture is in the form of a simple arch. The distal segment is broadly triangular in form. Embayments or invaginations occur in the dorsal surface of the distal segment, one on each side near the margins. That on the right side is more clearly seen than the one on the left owing to a slight anticlockwise twist in the specimen. The invaginations are situated towards the anterior of the segment and are bounded anteriorly by spurs which are seen immediately behind the second suture. From the lateral tips of the spurs, which form the antero-lateral angles of the segment, the margins are continued in a straight line towards the posterior tip of the segment. A remarkable feature, which has been seen in this specimen only, is the ornament of extremely fine striae which it exhibits. This is best seen on the right-hand side of the distal segment where the striae radiate across the surface of the segment from the inner margin of the invagination. Those striae, which extend anteriorly, cross the second suture without interruption and continue on the right postero-lateral portion of the middle segment. Striae which originate within the invagination at the posterior margin of the spur extend parallel to the edge of the segment in a posterior direction and then sweep diagonally across the rear part of the segment (text-fig. 4B; Pl. 43, fig. 1). Ornamentation can be traced also on the left posterior angle of the hastation, where striae radiate across the appendage from a point near the re-entrant angle at the rear of the hastation, and continue across the suture and over the left deltoidal plate. It would appear most probable that in life the entire surface of the appendage was sheathed in a fine integumen bearing striated ornament.

The 'median ridge' divides anteriorly into three lobes on the proximal segment of the appendage. There is a larger central lobe which does not extend forwards as far as the hastation, whereas the two lateral lobes almost reach the margins of the segment antero-laterally. The lobes unite at a point about one-quarter of the length of the segment from its posterior margin, and continue rearwards as a single median ridge which extends over the middle and distal segments. The margins of the ridge flare outwards at the sutures and it terminates posteriorly on the distal segment in two lobes.

The next growth stage is exhibited by the Kelvingrove specimens .09. 123. vq and .09. 123. vx. The latter (text-fig. 4C) has a length of 30·0 mm. and a maximum breadth of 8·0 mm. A similar growth stage is shown in R.S.M. 1865. 11. 11, Geol. Surv. 87287, Geol. Surv. Scot. 11825 and 11826. At this stage the shape of the appendage has already assumed the conical form of the adult, the point of greatest breadth being near the posterior of the proximal segment. The proportions of the segments and the form of the sutures are also similar to those of the adult. Differences occur, however, in the form of the post-lateral complexes, which are much simpler than in the mature appendage. The centre part of the distal segment is approximately semicircular in form, being bounded anteriorly by the median-curved portion of the second suture, and posteriorly by an almost straight margin. From this central region two lateral curved spurs or horns are developed from the distal segment, one on each side of the segment. They extend antero-laterally from the sides of the semicircular median part of the segment and then curve so that their tips are directed laterally or slightly post-laterally. Their anterior margins form a simple curve, convex towards the anterior, whereas the posterior margins are sigmoidal, the inner ends terminating near the median line of the appendage. The median-curved portion of the second suture terminates against the anterior margins of the spurs, and is presumably coincident with these margins as it is traced laterally.

Intermediate growth stages such as are shown in specimens Geol. Surv. 87288, 87289, and B.M. (N.H.) 59653, occur between that just described and the adult form. These, however, demonstrate only the constancy of the conical form of the appendage after the nepeonic stage has been passed, and a gradual increase in the complexity of the post-lateral regions.

The finest adult type B appendages seen are R.S.M. 1959. 35. 7 and Geol. Surv. Scot. 6643 (text-fig. 4E, F, G). Here the lateral horns of the distal segment, after growing antero-laterally, appear to curve fairly sharply until they are growing in a post-lateral direction. They extend post-laterally until their tips are posterior to the rear margin of the central part of the distal segment. In Geol. Surv. Scot. 6643 the appendage has been greatly flattened, and where the lateral spurs curve round from an antero-lateral to a postero-lateral direction they have been flattened upon themselves at the points of curvature, to form two round bodies (Pl. 43, fig. 6; text-fig. 4G). This is not seen in R.S.M. 1859. 35. 7, which has not suffered such severe flattening.

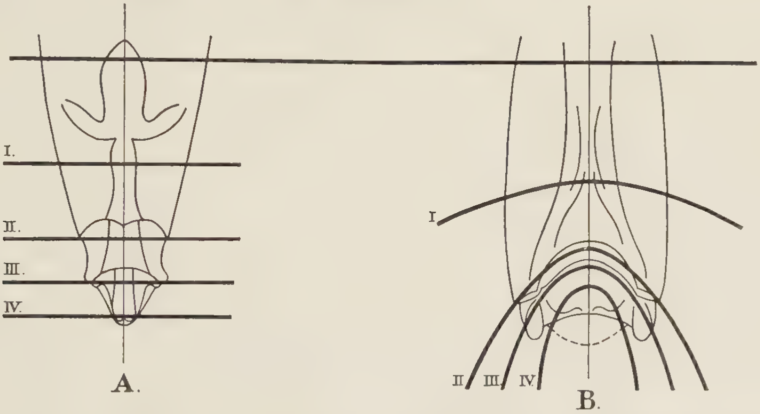
The lateral margins of the middle segment appear to extend posteriorly from the post-lateral angles of the proximal segment to the posterior part of the antero-lateral margin of the spurs of the distal segment. The supposition finds support in the simpler conditions seen in the juvenile forms (text-fig. 4C, D). A margin traverses the spurs of the distal segment and terminates laterally at the point where the lateral margins of the middle segment meet the distal spurs. This margin is rather indistinct and is interpreted by the writer as the posterior margin of the middle segment on the ventral side of the appendage. On the dorsal side, the posterior margin of the middle segment would appear in its lateral parts to coincide with the antero-lateral margin of the spurs of the distal segment. Another indistinct margin may be traced extending from the post-lateral angles of the proximal segment to a point just anterior to the position of curvature of the spurs of the distal segment. It is possible that this parallels the margin seen traversing the distal spurs and represents the posterior margin of the proximal segment on the ventral side of the appendage.

In summary, four features appear to be common to each of the post-lateral complexes of the adult type B appendage:

1. A distal member in a post-lateral orientation, which is regarded as a post-lateral extension of the spur of the distal segment clearly seen in juvenile forms.
2. Another member in a post-lateral orientation, lying anterior to the distal spur and posterior to the post-lateral angle of the proximal segment, which is thought to represent the lateral portion of the middle segment.
3. A margin traversing the posterior part of the distal spur, which is regarded as the posterior margin of the middle segment.
4. A margin traversing the middle segment between the post-lateral angle of the proximal segment and a point anterior to the position of curvature of the distal spur, which is regarded with hesitation as the posterior margin of the proximal segment on the ventral side of the appendage.

Although these features appear to be constant despite variation in the condition of preservation of the specimens, the interpretation of the structures presents many difficulties owing to the degree of specialization attained in *Slimonia*.

The form of the nepeonic type B appendage may be related to that of the adult appendage by the differential growth-rate diagram of text-fig. 5. The lines superimposed upon the outlines of the appendages have been constructed in the following ways. I, crosses the proximal segment three-quarters of its length from the anterior margin and is of purely diagrammatic significance. II, touches the post-lateral angles of the proximal segment, between which it crosses the middle segment. These points are not in doubt in either form. III, touches the post-lateral angles of the middle segment, between which it crosses the distal segment at the anterior margin of the invaginations. There is no difficulty in constructing this line in the nepeonic form, but to do so in the adult form requires the assumption that the spurs, which lie anterior to the invaginations and posterior to the second suture in the nepeonic appendage, become extended in the adult to form the posterior member of the post-lateral complex. If this is allowed, then the points about which the distal spurs are curved in the adult must represent the anatomical equivalent of the invaginations of the nepeonic form. IV, is a line crossing the posterior lobes of the distal segment. Support is given for the validity of the assumptions made in construction by the regular pattern which emerges in the resulting diagram. While the lines are parallel with and at right angles to the long axis of the appendage in the nepeonic form, they form a symmetrical series of curves in the adult which become more intense as the posterior of the appendage is approached. The adult form would therefore appear to be derived from the nepeonic form by greater differential growth at the margins of the distal part of the appendage as compared with a smaller growth-rate in the median region.



TEXT-FIG. 5. Diagram to illustrate the possible relationship through differential growth-rates of the form of the nepeonic (A) and adult (B) median abdominal appendage, type B, of *Slimonia acuminata* (Salter).

SEX AND FUNCTION OF THE APPENDAGES

While dimorphism of the median abdominal appendages of eurypterids is obvious, the determination of sex has proved difficult since no direct comparison can be made with closely related living forms. Following the work of Pocock (1902) on the secondary sexual characters among Xiphosura, and Gaskell's (1908) comparison of the opercular structures of eurypterids with those of *Thelyphonus*, Størmer (1934*a*) argued that the type A appendage was male and the type B female. He found support for this view principally in the secondary sexual characters seen in eurypterids such as clasping organs of *Mixopterus* and *Eurypterus*. More direct evidence became available in the wonderfully preserved genital appendages of the lower Devonian *Pterygotus rhenaniae* Jaekel, which is of particular interest for the present study, since the genital appendages of *Slimonia acuminata* may be compared closely with this form.

The type A appendage of *P. rhenaniae* is narrowly lanceolate and is made up of three segments (text-fig. 1). The form of the appendage is less specialized than in *Slimonia* but is very similar to the nepeonic condition of the Scottish species, particularly in the shape of the distal segment with its terminal incision dividing the posterior margin into two lobes. On the dorsal side of the German species, Størmer (1936) was able to detect a central aperture towards the posterior of the proximal segment which he regarded as probably the combined aperture of the *vasa deferentia*. This hypothesis is supported by the occurrence in *P. rhenaniae* of two parallel canals anterior to the opening. While no trace of *vasa deferentia* or genital aperture has been seen on the type A appendage of *Slimonia*, it may well be that the male aperture opened into the dorsal furrow which occurs on the proximal segment of the appendage in an equivalent anatomical position to the male gonopore of the German species.

The type B appendage of *P. rhenaniae* is broad and pear-shaped, and is also made up of three segments whose proportions are very similar to those of the adult type B appendage in *Slimonia* (text-fig. 3). Towards the posterior of the proximal segment, two fairly large ovate openings occur which may be ovipores. Similar openings have not been seen in *Slimonia*. On the other hand, post-lateral complexes, which are a specialized feature of the *Slimonia* type B appendage, have not been described from *P. rhenaniae*.

The comparison which can be made between the appendages of *Pterygotus rhenaniae* and *Slimonia acuminata* is sufficiently close to leave no doubt that the trispinate appendage of *Slimonia* is equivalent to the lanceolate appendage of *Pterygotus rhenaniae*, and Størmer's determination of a male sex for these appendages is here adopted. In the same way the similarities between the pear-shaped or conical appendages in both species are sufficient to prove their equivalence, and a female sex is presumed for this type. The differences in the more detailed features of the anatomy, however, suggest that the functioning of the appendages was distinct in the two species.

It is reasonable to suppose that the post-lateral complexes of the type B appendage of *Slimonia* may represent ovipositor mechanisms. This appears not unlikely when the longitudinal median structures of the proximal segment are considered. As has been stated above these structures have the appearance of two ducts or channels which pass posteriorly and laterally in ogee curves on either side of the hinder portion of the proximal appendage, and terminate in the region of the post-lateral complexes. These channels could be regarded as genital ducts leading to the post-lateral complexes. In *P. rhenaniae*, however, the ovipores are found on the proximal segment. If the post-lateral complexes of *Slimonia* are regarded as fulfilling an ovipository function, it is necessary to postulate the participation of the middle and distal segments in the female genital system, in addition to the proximal segment of the appendage. Laurie (1893) regarded the distal portion of the type B appendage of *Slimonia* as being eversible. The writer favours this suggestion because of the regular radial fold pattern that is found on the median part of the distal segment in nearly all specimens of the type B appendage. Were the distal part of the appendage eversible it would appear to favour the supposition that the function of the post-lateral complexes was ovipository.

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CHARLES D. WATERSTON
Royal Scottish Museum,
Edinburgh

Manuscript received 8 July 1959

A NEW ECHINOID FROM THE LOWER CRETACEOUS (ALBIAN) OF KENT

by RAYMOND CASEY

ABSTRACT. *Holaster cantianus* sp. nov. is a large holasterid of Lower Cretaceous (Lower Albian) age and is found in the Lower Greensand (Folkestone Beds) of the Folkestone neighbourhood of Kent. It is designated type species of a new subgenus, *Labrotaxis*, to which is also referred the Upper Albian–Cenomanian *Holaster latissimus* J. L. R. Agassiz. The diagnostic feature of *Labrotaxis* is the primitive condition of the meridosternous plastron.

THE common occurrence of a large echinoid belonging either to *Holaster* or to *Cardiaster* in the Folkestone Beds (Lower Albian) of the Folkestone neighbourhood of Kent has long been known (Price 1874; Topley 1875; Casey 1949), but owing to the imperfect state of preservation of the specimens no attempt at specific determination or description has been hitherto made. The following account is based on material accumulated by the author over a period of many years and now incorporated in the collections of the Geological Survey Museum, London. The paper is published by permission of the Director of the Geological Survey and Museum.

Order HOLASTEROIDA Wyatt Durham and Melville 1957
Family HOLASTERIDAE Pictet 1857
Genus HOLASTER J. L. R. Agassiz 1836
Subgenus LABROTAXIS nov.

Type species. *Holaster* (*Labrotaxis*) *cantianus* sp. nov.

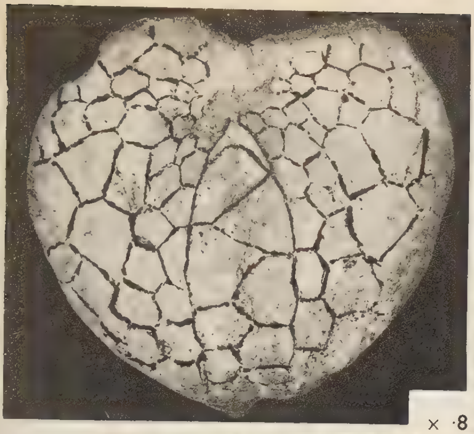
Diagnosis. *Holaster* with well-developed frontal sulcus bounded by carinae. Plastron of primitive meridosternous type, the labrum spanning the oral margin of sternal 2′ to make contact with sternal 2.

Remarks. Among the Spatangoida and the Holasteroida the structure of the plastron has high taxonomic value. In the former order it is of amphisternous type, characterized by the labrum being joined at its posterior end to two large, equally developed sternal plates (2′, 2). The Holasteroida include those forms in which the plastron is meridosternous, with the labrum abutting against a single sternal plate (2′). Lambert (1893) showed that in *Holaster intermedius* (Münster), of very early Cretaceous (Neocomian)

EXPLANATION OF PLATE 44

Figs. 1–4, *Holaster* (*Labrotaxis*) *cantianus* sp. nov., Lower Greensand (Folkestone Beds), Folkestone, Kent. Author's collection, now in the Geological Survey Museum, London. 1, Adoral surface, the sutures inked-in. Zm 32, reduced ×0·8. 2, Part of adapical surface showing pores and ornament. The apical system lies on the right-hand border of the photograph; the frontal sulcus runs obliquely upwards. G.S.M. 97304, enlarged ×5. 3, Two of a group of three specimens (the third is on the other side), the larger being the holotype. G.S.M. 74118–19, natural size. 4, Smaller specimen illustrated in fig. 3 enlarged ×2.

[Palaeontology, Vol. 3, Part 3, 1960, pp. 260–4, pl. 44.]



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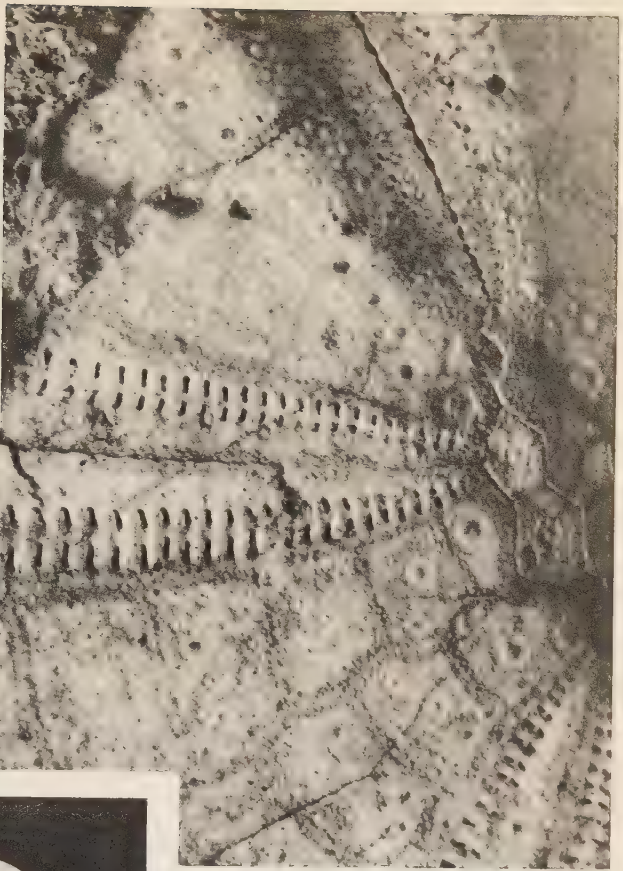

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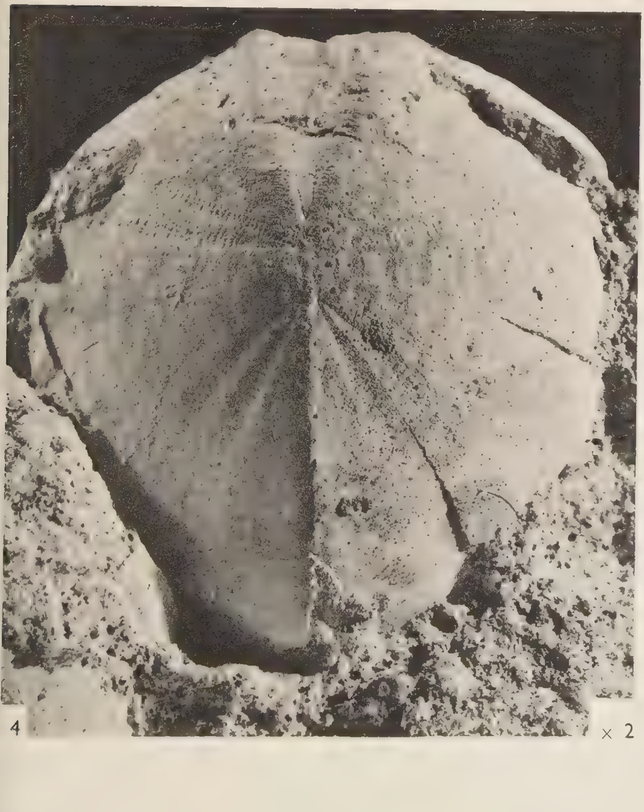

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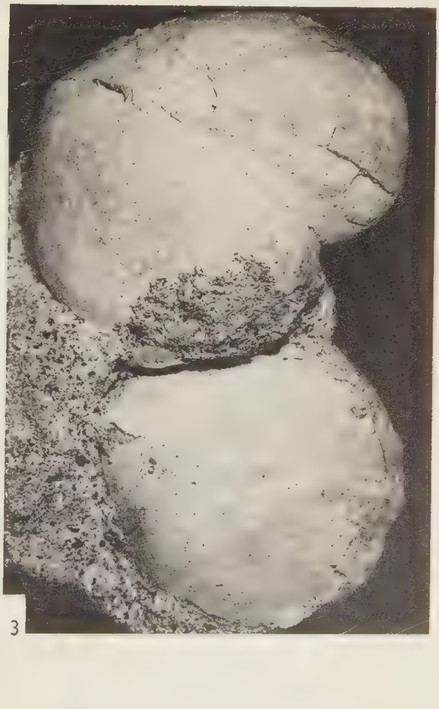

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CASEY, *Holaster (Labrotaxis) cantianus*

age, the meridosternous type of plastron is already typically developed, the labrum being well separated from the second sternal plate (2). His illustrations of the plastron of *H. nodulosus* (Goldfuss), the type species of *Holaster*, from the base of the Upper Cretaceous, show this second sternal plate even farther removed from the labrum, its position behind sternal plate 2′ foreshadowing the single row of plastronal plates peculiar to the subgenus *Sternotaxis*. On the other hand, the plastron of *Labrotaxis* (Pl. 44, fig. 1; text-fig. 1*d*), having the labrum just touching sternal plate 2, represents a more primitive stage in the evolution of the meridosternous condition than is seen in *H. intermedius*. In all other features, especially the intercalary type of apical system, *Labrotaxis* conforms to the Holasteridae. It lacks the ambital fasciole of *Cardiaster* and the sharp frontal carinae and unequal pores of *Pseudholaster*. An Upper Albian–Cenomanian form, *H. latissimus* J. L. R. Agassiz, is also referable to *Labrotaxis* and the scope of the subgenus may be expected to widen with increasing knowledge of the plastronal structure of other members of the genus.

Holaster (*Labrotaxis*) *cantianus* sp. nov.

Plate 44, figs. 1–4; text-fig. 1

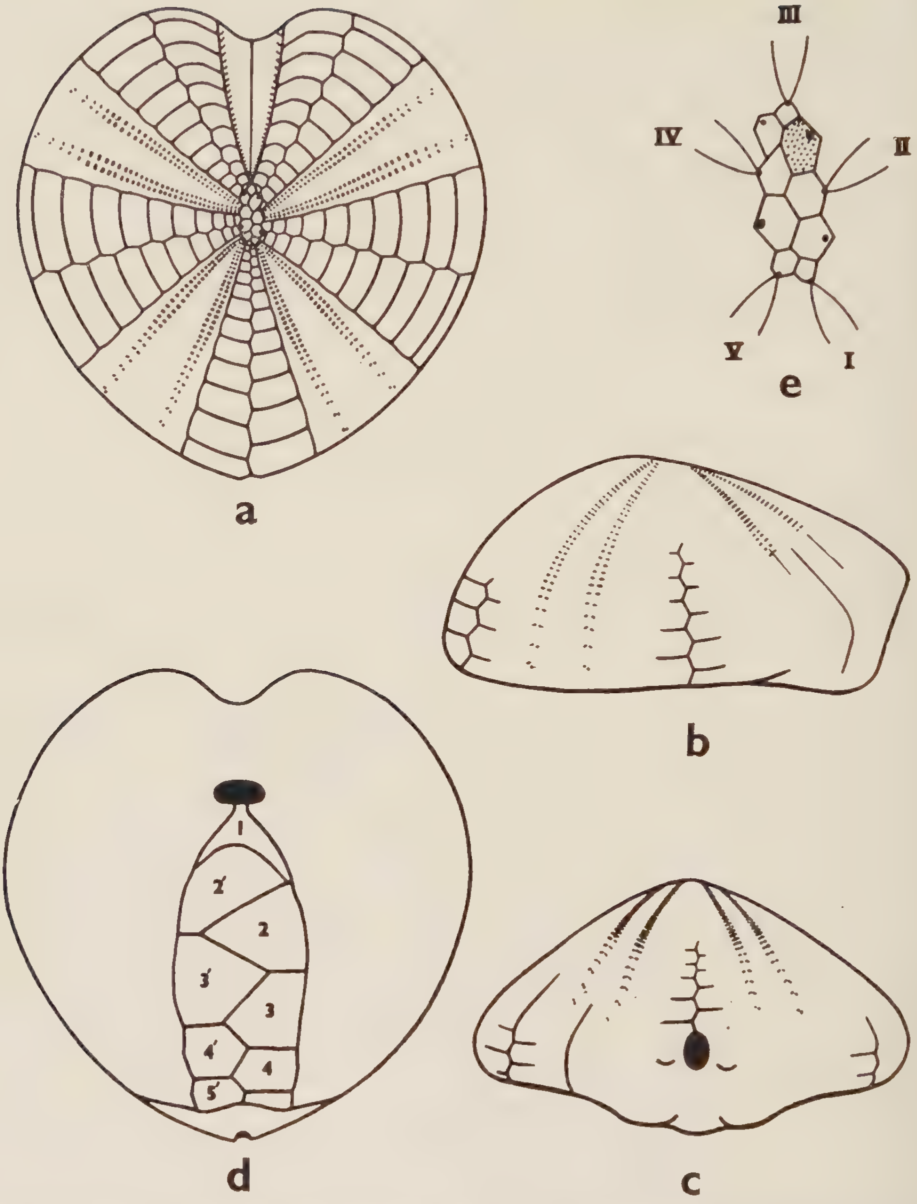
Holaster sp., Price 1874, p. 140.
? *Holaster*, Topley 1875, p. 138.
Cardiaster ? sp., ibid., p. 413.
Holaster, large undescribed species, Casey 1949, p. 225.

Holotype. G.S.M. 74118, Lower Greensand (Folkestone Beds) (Lower Albian, *tardefurcata* Zone, *regularis* Subzone), East Cliff, Folkestone, Kent.

Description. Test large (up to 70 mm. long), fairly thin, of heart-shaped outline, widest at the anterior three-fifths of the length and contracting posteriorly, the length slightly exceeding the width. Adapical surface elevated, the highest point of the test placed well forward, at the apical system or just in front of it. From the anterior border the profile makes a sweeping curve to the summit and thence declines in a gentle curve to the posterior border, which is truncated either vertically or obliquely downwards and inwards. A cross-section of the test through the summit is subtrigonal in outline, with the sides and base nearly flat, but rounded at the ambitus and the apex. Posterior to the summit the sides of the test are gently vaulted, the line of their convergence being marked by a faint carina extending from the centre of the disk to the posterior extremity. Anterior border indented by the frontal sulcus, which is defined by two blunt carinae diverging at an angle of 25° from their point of origin at the apical system. Periproct oval, placed high in the concave posterior face.

Adoral surface more or less flattened, depressed around the peristome, which is very eccentric anteriorly, transversely oval and without a labral process. Plastron tumid, increasing in elevation posteriorly, with about seven ill-defined nodules connected into a zigzag. Nodules also on either side of the periproct and at the base of the posterior face and a line of them, albeit faint, is traceable on each of the frontal carinae.

Ambulacral areas fairly wide, the paired ambulacra subpetaloid. Near the apex the ambulacral plates are raised a little at the median vertical sutures, giving a sunken appearance to the poriferous avenues on that part of the test. The pairs of poriferous avenues have a simple adoral divergence, and the pores are uniserial, subequal, and feebly conjugate. Pore-pairs in ambulacra I, II, IV, and V close to the adradial suture



TEXT-FIG. 1. *Holaster* (*Labrotaxis*) *cantianus* sp. nov. *a*, *b*, *c*, diagrammatic representation of specimen viewed from top, side, and posterior end; based on G.S.M. 74118–21. *d*, under surface showing plating of the plastron, with the labrum (1) spanning the oral margin of sternal plate 2′ and touching sternal plate 2; G.S.M. Zm 32. *e*, apical system; G.S.M. 97304. *a–d* approximately natural size, *e*×4.

near the apex, remote at the ambitus, the pores slit-like and nearly horizontal, becoming rapidly smaller, closer, and circumflex towards the ambitus. Poriferous avenues in ambulacra II and IV unequal, the anterior series having smaller and more approximated pores. Poriferous avenues of ambulacrum III lodged in the sides of the sulcus and adjacent to the adradial suture, the pores minute and oblique.

Apical system elongate, composed of angular plates flush with the surrounding corona. Oculars II and IV meet in the mid-line and separate the anterior from the posterior genitals. Oculars II and IV and genitals 1 and 4 each support a tubercle. Madreporite covers all of genital 2.

Interambulacral areas built up of long curved plates, averaging eleven plates to a column from apex to ambitus. Plastron composed of a series of alternating cuneiform plates surmounted by an asymmetric, subtrigonal labrum, conforming to the characters of the subgenus.

All plates finely granulate, those of the upper surface studded irregularly with very small tubercles which become larger and more thickly clustered towards the anterior carinae and around the apical system, and larger still along the sides of the sulcus. A line of miliaries, sometimes irregular or failing at the ambitus, runs vertically up the sulcus, parallel and close to each of the inner lines of pores in ambulacrum III. Most of the lower surface is covered with primary tubercles. On the plastron the tubercles are crowded and are graduated in size, the smallest at the centre of the plastron, the largest at the margins. Periplastronal areas devoid of tubercles. The tubercles have crenulated bosses, perforated summits, and wide scrobicular circles limited by the granules.

Remarks. This echinoid is ubiquitous in the Folkestone Beds of the Folkestone district, ranging from the *jacobi* Subzone of the *nodosocostatum* Zone to the *mammillatum* Zone. The holotype is one of three specimens found in association in the *regularis* Subzone, on which horizon the species reaches its maximum. Specimens used in this account are listed below under the registration numbers of the Geological Survey Museum:

97304 *mammillatum* Zone (top stone band), Copt Point, Folkestone, Kent.
74118–20; 74121 *tardefurcata* Zone (*regularis* Subzone, 15–25 ft. below 97304), East Cliff, Folkestone.
Zm 32, 35 *tardefurcata* Zone (*regularis* Subzone, bottom stone band), as before.
97305 *tardefurcata* Zone (*regularis* Subzone), Mill Point, Folkestone.
97306 *tardefurcata* Zone (*trivialis* Subzone), Sandling Junction sandpit, Hythe, Kent.
Zm. 522, 653 *nodosocostatum* Zone (*jacobi* Subzone, Red Bed), as before.

Holaster (*Labrotaxis*) *latissimus* Agassiz is a more orbicular species with rather more pronounced anterior carinae; the profile lacks the posterior descent of *H.* (*L.*) *cantianus*, tuberculation is not so strong on the apex, and the ambulacral plates are more numerous, the poriferous avenues generally narrower. Unlike the Cenomanian form figured by d'Orbigny (1853, pl. 387–8), the English Upper Albian specimens of this species are less elevated than *H. cantianus* (cf. Wright 1878, pl. 67, fig. 2*b*). *Holaster amplus* d'Orbigny, described from the Albian of Grandpré (Ardennes), France, and united with *H. latissimus* by Desor (1858, p. 337), is an orbicular, depressed form with long, sloping posterior end. The earlier Lower Greensand forms, *H. benstedi* Forbes (Lower Aptian) and *H. wrighti* Lambert (Upper Aptian), like the foreign Aptian *H. cordatus* Dubois and *H. prestensis* Desor, are much smaller and more rotund.

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R. CASEY
Geological Survey and Museum,
London, S.W. 7

Manuscript received 20 June 1959

CALATHOSPERMUM FIMBRIATUM SP. NOV., A LOWER CARBONIFEROUS PTERIDOSPERM CUPULE FROM SCOTLAND

by P. D. W. BARNARD

ABSTRACT. A new cupule generically comparable to *Calathospermum scoticum* Walton is described containing ovules identical in form to the seeds known as *Salpingostoma dasu* Gordon. The specimens of this new species illustrate some interesting morphological features new to the genus. The cupule is believed to be equivalent to a large part of a frond and its branching may be interpreted as a pinnate system.

THE material on which these observations are based consisted originally of a block of volcanic ash containing petrified plant remains. It was collected by the late Professor W. T. Gordon. The plants so far described from this source are *Tetrastichia bupatides* Gordon (1938), *Salpingostoma dasu* Gordon (1941), and *Eosperma oxroadense* Barnard (1959). The present communication concerns a large cupule belonging to *Calathospermum* Walton (1940) which is believed to have borne *Salpingostoma dasu* seeds.

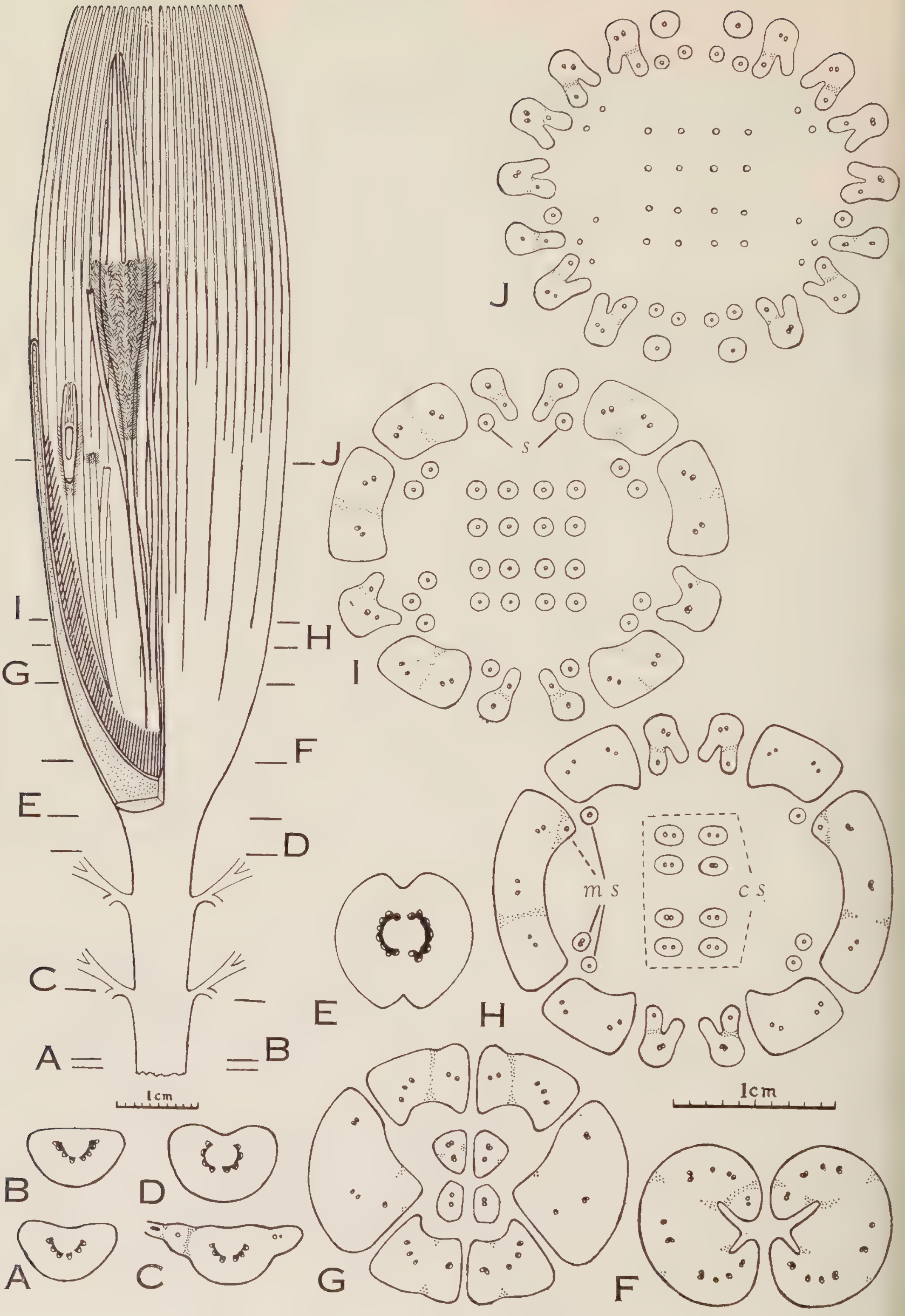
The various fragments of the original block of ash, now broken and cut up, have yielded more than ten specimens of this new cupule. Three of these were sectioned by Gordon who prepared thirty-two petrological slides, some of which were lent to Professor J. Walton who at the time was describing *Calathospermum scoticum*. The series, however, did not permit a detailed description, but Walton noted that Gordon's specimens differed from *C. scoticum* in having more divided cupule segments and in having a different vesture. The remaining specimens have been examined by the peel technique of Lacey and others (1956). Rock slices of specimens of *Salpingostoma dasu* not used by Gordon in preparing petrological sections were also examined by the peel technique. Some new specimens of *S. dasu* have also been discovered in the course of these studies.

GENERAL MORPHOLOGY

The cupule is believed to have been borne terminally on the main (primary) rachis of what was probably a special fertile frond (text-fig. 1). Below the cupule the primary rachis, which probably exceeded 7 cm. in length, bore two rows of opposite pinnae at intervals of 10–12 mm. In transverse section the primary rachis is nearly flat adaxially and strongly convex abaxially and measures 6 mm. in width by 3 mm. in height (text-figs. 1, 2A–D). The pinnae on the primary rachis are divided near their base into three portions, possibly the bases of pinnules.

The cupule itself is divided into two halves which may correspond to the two main arms (secondary rachises) typical of many pteridosperm fronds. The base of the cupule would thus be equivalent to the region of bifurcation (text-fig. 1F). Within 3 mm. or so of its origin the secondary rachis gives rise to a pair of lateral pinnae and ends in a terminal pinna (text-fig. 1G). These (primary) pinnae form the basic segments of the cupule.

[Palaeontology, Vol. 3, Part 3, 1960, pp. 265–75, pl. 45.]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Each primary pinna or segment bears in turn about five secondary pinnae alternately; of these, the two proximal appear to have been fertile, and the three more distal, vegetative. The rachises of the fertile pinnae may branch dichotomously and may bear from one to four ovules. In *Calathospermum scoticum* the seed stalks (fertile rachises) which arise from a single axis at the base of the cupule were called collectively the central (stalk) system by Walton. This term is used here for the rachises of the four fertile pinnae which arise from the bases of the lateral primary pinnae. The marginal system in *C. scoticum* is here represented by the remaining fertile pinnae. The sterile secondary pinnae branch in an alternate manner and end in from three to five or sometimes more ultimate, uninerved, cylindrical processes (pinnules) which I have called strands (*s* in text-figs. 1, 3). As shown in the reconstruction (text-fig. 1), some of these strands exceed 5 cm. in length and have an average diameter of 1 mm. The tip of the cupule was not preserved in any of the specimens examined so that the exact total length is uncertain. In all but one of the specimens examined the rachises of both the central and marginal systems as traced upwards become poorly preserved and shrunken in appearance and apparently end some 2 to 3 cm. above their origin.

Recognizable attached ovules, two of which are shown in (text-fig. 3C, D), have only been seen in one specimen (no. 2); this contained at least three and probably four small, poorly preserved ovules. Two of them belonging to the marginal system are borne terminally on the undivided rachises of fertile pinnae. One of these (text-fig. 3C) arises from the abaxial margin of the terminal pinna and the other from a lateral pinna. The stalk of the third ovule (text-fig. 3D) had its origin on the left abaxial lateral pinna, and separated from it at a level in between that of the lowest fertile pinna rachis and that of the first strand (*a* in text-fig. 3A). It does not appear to have affected either of the two 'branches' between which it is interpolated.

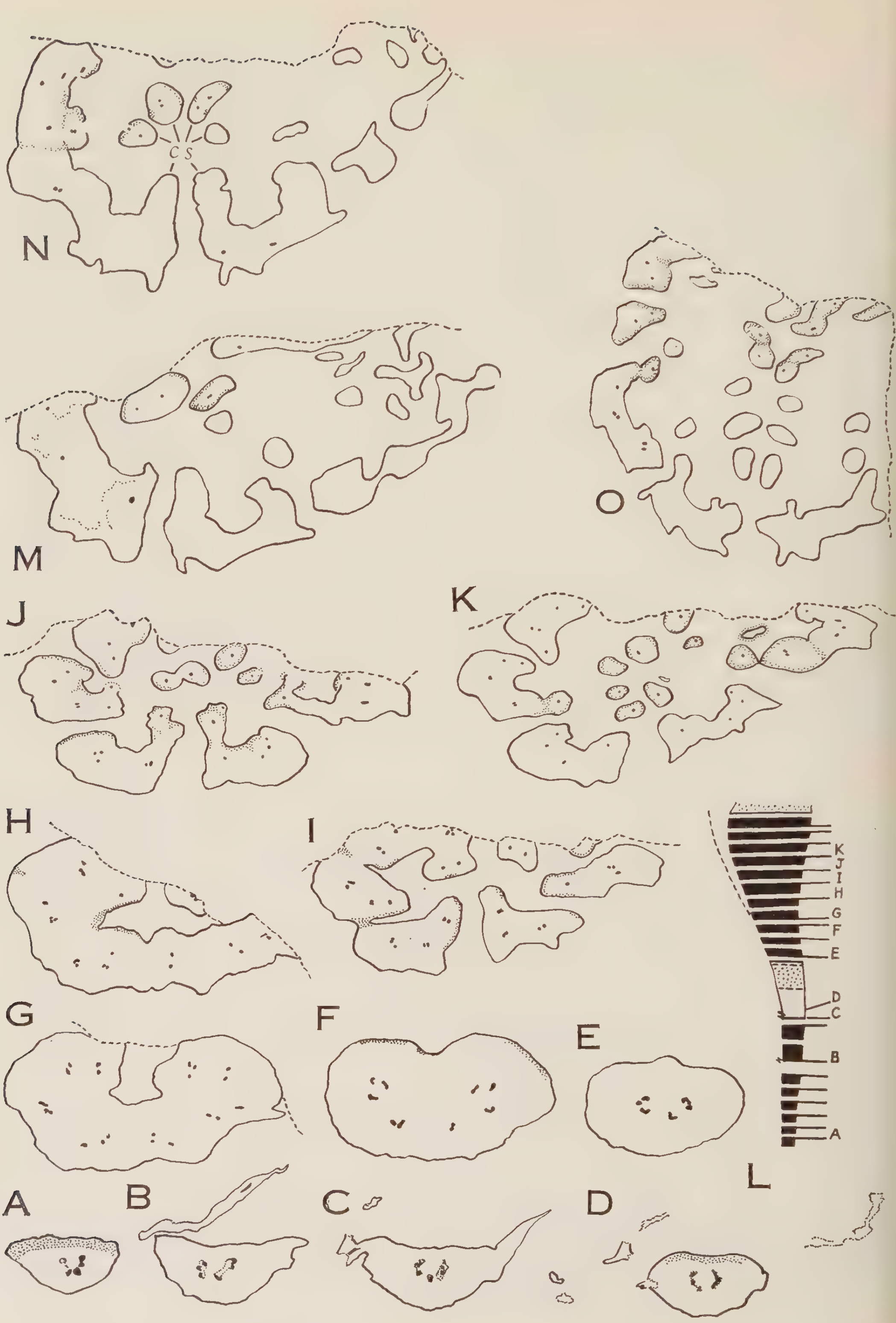
ANATOMY

The epidermis. As seen in surface sections of the rachis the epidermal cells are mainly rectangular, though some have an inclined end wall, and others are five-sided with a gable end. When seen in transverse section they appear nearly square, and in radial longitudinal section, rectangular. The average dimensions are: length, 102 μ; radial height, 34 μ; tangential width, 38 μ. Stomata appear to be present on the primary rachis (text-fig. 4A, B). They may also have been present on the outside of the cupule lobes.

In the lowest 3 cm. of the cupule, large epidermal hairs with an average diameter of 45 μ are found on the inside of the segments and their subdivisions. They are very long, straight, and without apparent cross walls. I estimate that they were at least 5 mm. long and may even have exceeded 10 mm.

Fine epidermal hairs, with an average diameter of 13 μ, are present around a few of the seed stalks and also around the ovules in specimen 2 (text-fig. 3B; Pl. 45, fig. 5).

TEXT-FIG. 1. *Calathospermum fimbriatum* sp. nov. Reconstruction of the frond with a quarter of the cupule cut away to reveal the contents; the fertile rachises, one bearing an ovule shown in section and another a *Salpingostoma* seed; together with transverse sections A to J through the regions indicated. In section H, *ms*, the fertile rachises of the marginal system (on the left only); the fertile rachises of the central system are inclosed —*cs*—. In section I, *s*, strand.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Similar hairs occur in *Salpingostoma dasu*, where they are found on the body of the seed and on its stalk, but only for some 5 to 10 mm. below the base of the seed.

The cortex. This is differentiated into two distinct zones, an inner parenchymatous ground tissue, and an outer fibrous zone or sterome.

The sterome is composed of a number of rows of longitudinally elongate cells of small diameter and fairly thick walls. The average dimensions are: length, 500 μ+; diameter, 33 μ; wall thickness, 4 μ. The sterome is broken radially by numerous gaps with such an irregular disposition that it cannot be called a 'sparganum'. Some of these gaps appear to underlie stomata in the epidermis.

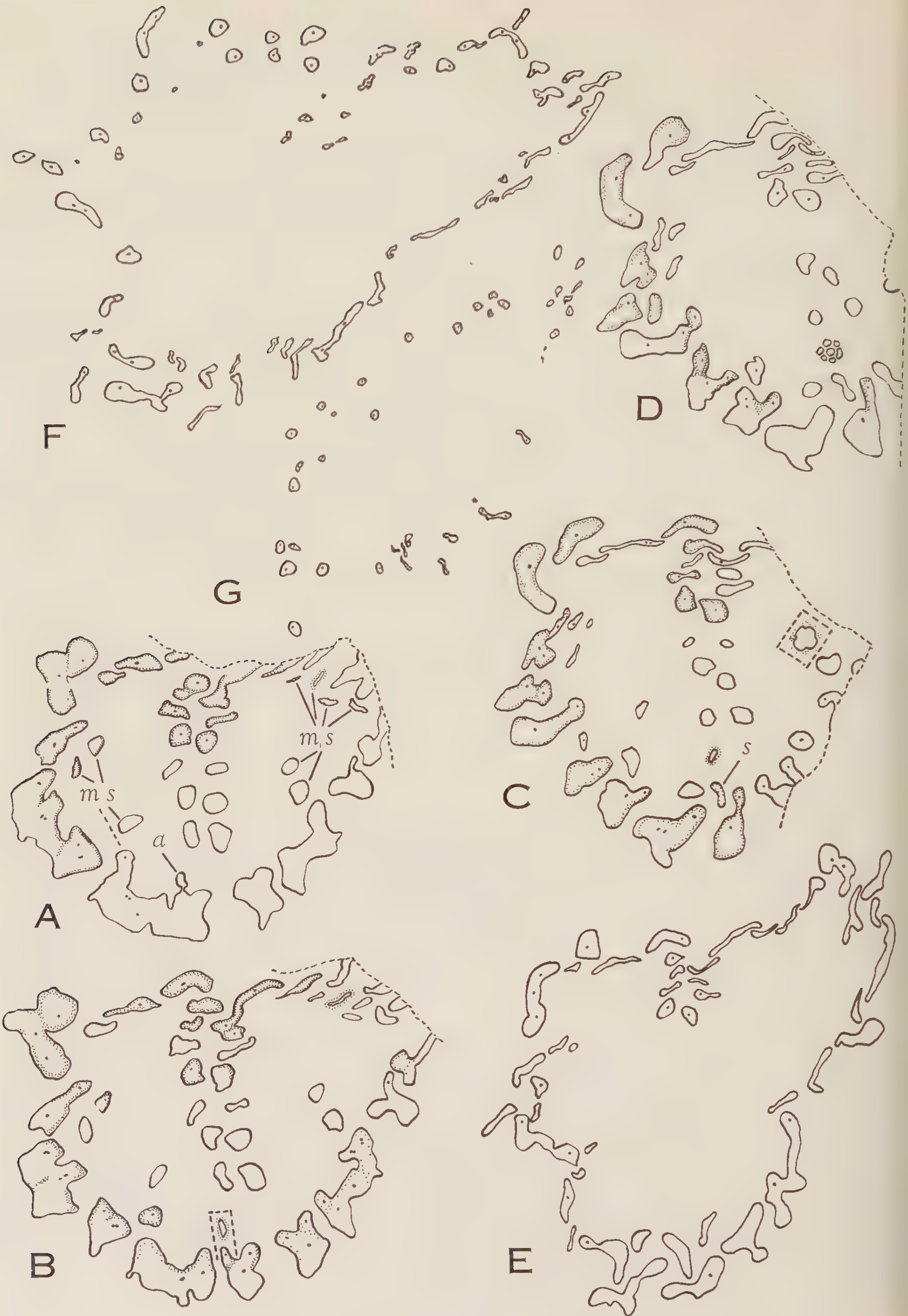
The distribution of the fibres is probably related to the mechanics of the cupule: thus in the primary rachis the sterome is generally better developed abaxially than adaxially; it is greatly reduced in the conical base of the cupule, but increases again all round after the primary division into segments, only to decrease again in the pinnules. The sterome thickens in the base of the seeds as indicated by Gordon.

The ground tissue consists of large empty isodiametric parenchyma cells about 100 μ in diameter, amongst which are scattered slightly larger 'secretory' cells with black, often crystalline contents, and nests of somewhat similar cells which are surrounded by clear parenchyma cells which are somewhat radially elongate with respect to the centre of the nest. These nests of dark cells occur very regularly in the adaxial groove in the xylem of the primary rachis, and give a scalariform appearance to longitudinal sections, but elsewhere their distribution is more random.

The vascular system. The xylem of the vascular bundles is often extremely well preserved whilst the phloem cannot be discerned, but it may be represented by part or all of the cavity surrounding the xylem. The xylem is mesarch and consists of annular protoxylem tracheids, reticulate to pitted centrifugal tracheids, and pitted centripetal tracheids (text-fig. 4C and D), with pits about 7 μ in diameter, distant and the pit apertures horizontal and opposite. The tracheids range in diameter from 14 μ (protoxylem) to 40 μ (metaxylem).

In the primary rachis the bundle was probably a continuous U-shaped strand, though as seen now it is always irregularly broken especially at the bottom. The xylem contains from 6 to 8 protoxylem groups, one situated in each of the abaxial ridges of the strand. The most abaxial pair of protoxylem groups divide just above the 'pinna node' and the new groups so produced depart from the central bundle to form separate traces which run parallel to the parent bundle until they pass into the pinnae at the next 'node'. As they pass out they divide to form two xylems of unequal size, the larger of which soon divides again.

TEXT-FIG. 2. *Calathospermum fimbriatum* sp. nov. A–K, Series of transverse sections (specimen 1) showing the origin of the lateral pinnae on the primary rachis, and the basal segmentation of the cupule. Owing to the slightly oblique nature of the sections the fertile rachises of the central system depart from the adaxial primary pinnae between I/J and the abaxial primary pinnae between J/K. A, G.C. 2190; B, G.C. 2196; C, G.C. 2198; D, G.C. 2203 (peel 23); E, G.C. 2207; F, G.C. 2209; G, G.C. 2210; H, G.C. 2211; I, G.C. 2212; J, G.C. 2213; K, G.C. 2214; L, restored outline of the same specimen to show the position of the petrological sections and the small portion peeled. The letters A to K indicate the sections illustrated. M to O, basal sections of a series of oblique transverse sections (specimen 2) continued in text-fig. 3. In N, *cs*, fertile rachises of the central system. Owing to the oblique nature of the section the adaxial rachises are shown above their first division whilst abaxially they are still attached. M, G.C. 2218; N, G.C. 2221; O, 2223. All ×3, except L×1.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As the primary rachis enlarges into the base of the cupule the strand divides to give two C-shaped portions, each of which then breaks up into three; its further subdivisions follow those of the cupule. Each division of the xylem occurs at a distance of from 5 to 15 mm. below that at which the individual parts of the cupule they supply become free from one another. The strands and the fertile rachises contain a single oval xylem bundle with an excentric mesarch protoxylem. Re-examination of the stalks of *Salpingostoma dasu* revealed a single oval xylem bundle in three specimens. This is shown in Gordon's pl. 1, fig. 6, but it is rather obscured in that specimen by the pyrite. The single oval bundle when traced upwards into the seed becomes horseshoe-shaped (Gordon's term) before dividing to produce the six oval integumentary bundles.

CORRELATION WITH *SALPINGOSTOMA*

There are three reasons for relating the seed *Salpingostoma dasu* to this cupule: the discovery of small ovules in some of the cupules, the presence of fine hairs in some of the other cupules, and the close histological similarity.

The best ovule is shown in text-fig. 3D, where one can clearly see the apical processes. Unfortunately the body of this ovule was lost in the preparation of petrological sections. Its stalk, surrounded by a belt of fine hairs, is shown in Pl. 45, fig. 5.

When traced upwards the seed stalks in the cupules become collapsed and poorly preserved just before they disappear. The stalks of *Salpingostoma* seeds fade out similarly downwards. I believe that rupture of the stalks was not confined to a specialized abscission zone, but rather that it occurred at any weak point. Most of them appear to have parted in the hairless region, but an occasional one broke slightly higher so as to eave part of the hairy region in the cupule.

The approximate dimensions of the ovules is shown in the table alongside those of *C. scoticum* and *S. dasu* after Walton (1949).

	Salpingostoma	*Calathospermum*	
	dasu	*C. fimbriatum*	*C. scoticum*
Number of tentacles	6	6	9+
Length of ovular body	14 mm.	3·5 mm.	3 mm.
„ „ tentacles	25 mm.	4 mm.+	12 mm.
Diameter of ovular body	6 mm.	1·2 mm.	1·9 mm.
„ „ tentacles	1·2 mm.	0·25 mm.	0·21–0·25 mm.
„ „ lagenostome	1·6 mm.	0·6 mm.	1·4 mm.
„ „ salpinx	0·4 mm.	0·3 mm.	0·47 mm.
„ „ hairs	12–20 μ	10–15 μ	12–14 μ

That the size differences may be due to differences in maturity was mentioned by Walton. In this instance it would appear probable that the ovules were abortive and

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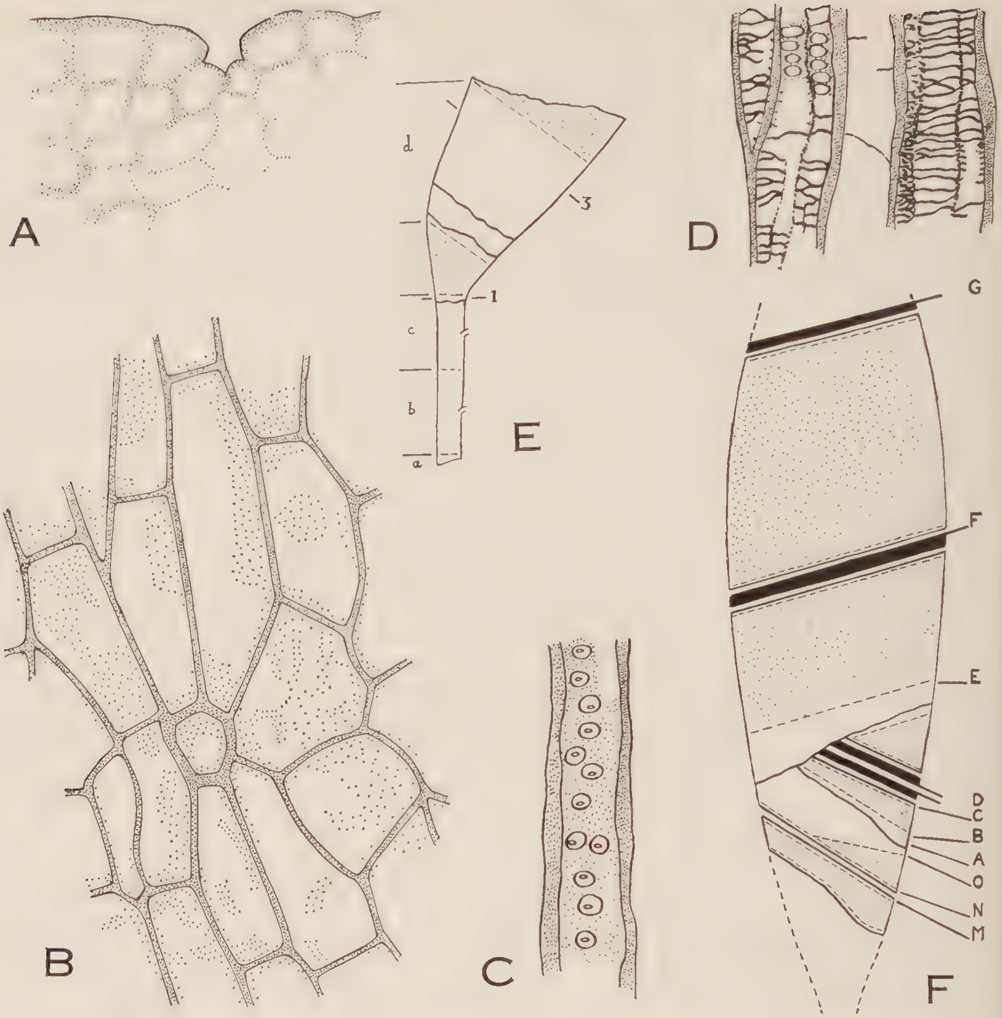
TEXT-FIG. 3. *Calathospermum fimbriatum* sp. nov. A–G, Continuation of the series of oblique transverse sections (specimen 2) commencing in text-fig. 2M. A, Showing *a*, the anomalous departure of the stalk of an ovule from the left abaxial primary pinna (segment); *ms*, fertile rachises of the marginal system. G.C. 2225. B, The first vegetative secondary pinna has now separated from the left abaxial segment. The ovule stalk surrounded by the interrupted line is shown in Pl. 45, fig. 5. G.C. 2229. C, Showing he body of an ovule of the marginal system sectioned medinally; it is illustrated again in Pl. 45, fig. 6. The left abaxial segment is now represented by three secondary pinnae, from one of these a strand *s* has separated. G.C. 2235. D, Petrological section showing the six tentacles and lagenostome of the ovule with the anomalous stalk attachment. G.C. 2236. E, G.C. 2245. G, G.C. 2248. All ×3.



TEXT-FIG. 4. *Calathospermum fimbriatum* sp. nov. A, Transverse section of primary rachis showing epidermis with probable stoma and a portion of the sterome. G.C. 2282 (peel 6), ×250. B, Surface section of primary rachis showing epidermis with probable stomatal pit. G.C. 2283 (peel 1), ×250. C, Radial longitudinal section of pitted centripetal tracheid. G.C. 2286 (peel 57), ×300. D, Radial longitudinal section of reticulate to pitted centrifugal tracheids. G.C. 2285 (peel 52), ×300. E, Restored outline of holotype to show extent of specimen and regions peeled, unpeeled portion stippled; transverse series *a*, 10 peels; *c*, 60 peels and *d*, 88 peels; *b*, longitudinal series of 100 peels. 1 and 3 indicate positions of sections illustrated in Pl. 45, figs. 1, 3, ×1. F, Restored outline of specimen 2 to show the positions of the petrological sections, regions peeled, and the positions of the sections in text-figs. 2, 3, ×1.

that the mature seeds had been shed. A few small detached seeds the same size as the ovules in the cupule have been discovered in the course of this investigation. It is possible that these could be the seeds of this cupule and *S. dasu* the seeds of a different and possibly larger cupule. One of these new seeds contained microspores (? pollen) in its lagenostome (Pl. 45, fig. 7). Large quantities of similar microspores, many of them still adhering in tetrads and in larger masses, are present in cupule specimens 2 and 3. The single seed found containing microspores might, therefore, represent a post-pollination stage ovule which became detached preventing further development.

The histology of *S. dasu* differs from that of the cupule in only two minor details. The xylem in *Salpingostoma* was only observed to consist of annular and reticulate (scalariform) tracheids, whereas in the cupule rachis pitted forms were also present. The megaspore membrane of *S. dasu* as revealed by maceration of a small portion of Gordon's seed no. 8 (Pl. 45, fig. 8) is similar to that found in one of the new small seeds, except that the fibrils of the membrane are more widely separated (expanded) and the meshes of the cellular reticulum on the outer surface are approximately 350 μ as compared to 250 μ in the smaller seed.

Genus CALATHOSPERMUM Walton 1940

Emended diagnosis. Cupule borne terminally on a dorsiventral rachis and containing numerous stalked ovules. Cupule consisting of six main segments which may be simple or divided. Ovules borne terminally on rachises which arise marginally on the segments or from the base of the cupule or from both. Ovules similar to the seeds of the type known as *Salpingostoma* Gordon 1941.

Calathospermum fimbriatum sp. nov.

Plate 45, figs. 1–7

Cupule about 90 mm. long and 30 mm. broad at its widest part, borne on a primary rachis 6 by 3 mm. in diameter. Cupule bilaterally symmetrical and divided into equal halves from just above the base, each half again divided into three segments. Each segment subdivided into five pinnae, the two basal of which are seed-bearing, and the three higher sterile. Fertile pinna rachises with from one to four ovules. Sterile pinnae ending in three or more strands, 1 mm. in diameter.

Material. Holotype specimen no. 5, slide nos. 2279 to 2330; Gordon collection, Geology Department, King's College, London: and paratypes slides nos. 2190 to 2385; together with peel collection and rock specimens from the Green Ash within the Cementstone Group (Upper Tournaisian) of the Calciferous Sandstone Series (Lower Carboniferous) at Oxroad Bay, in East Lothian, Scotland.

Discussion. The view adopted here that *C. fimbriatum* is a modified frond is the one advanced by Walton in 1949. This appears fully justified by the morphology and anatomy of the cupule stalk in *C. fimbriatum* which is unquestionably a rachis. If only an isolated portion of such a stalk had been found (e.g. Pl. 45, fig. 2) it would have been described as a rachis and placed in the form genus *Lyginorachis*.

Some light may be thrown on the question as to whether the stalk is a primary or secondary rachis by comparison with *Lyginopteris oldhamia* (Binney) as described by C. Louvel (1959), and *Tetrastichia bupatides* Gordon (1938). In *L. oldhamia* the primary rachis (petiole) bears opposite pinnae and above the bifurcation the secondary rachises bear alternate pinnae. The primary rachis contains a W-shaped xylem strand formed by the partial fusion of two V-shaped traces which supply the secondary rachises. In *T. bupatides* there are no pinnae on the petiole (primary rachis); on the secondary rachises the pinnae are alternate (original observation). In the petiole the xylem strand is butterfly shaped (a modified W) and separates into two modified V-shaped traces at the bifurcation.

In comparing the two species of *Calathospermum* a number of differences become apparent. The cupule segments in *C. scoticum* are not pinnately divided yet they contain six xylem strands. The seed-bearing branches of the central system in *C. scoticum* arise from a central stalk which appears as a direct continuation of the primary rachis (cupule stalk), and the marginal system is more extensively developed in that twelve pinnae contribute to it as opposed to the eight in *C. fimbriatum*. The four extra pinnae in *C. scoticum* arise from the lateral pinnae (cupule segments). In *C. fimbriatum* (specimen 2) the ovule which arises in an anomalous position appears to be a homologue of one of the extra marginal pinnae in *C. scoticum*.

The two cupules also differ markedly in their relative proportions. The cupule of *C. fimbriatum* is twice as long as that of *C. scoticum* and the diameters of their stalks are in the same proportion. However, the diameters of the two cupules are about equal. The fertile rachises in *C. fimbriatum* arise over a distance of about 9 mm., whereas in *C. scoticum* they all arise within 3 mm. of one another. These proportional differences suggest the following explanation for some of the morphological differences: that the number of fertile pinnae per cupule is determined by some factor correlated with growth in diameter, and that the basal origin of the central system in *C. scoticum* is due to a telescoping of the region over which the fertile pinnae arise.

Walton (1949) has compared *C. scoticum* and *Diplopteridium tielianum* (Kidston) Walton. It is interesting to note that the frond of *C. fimbriatum* appears to be intermediate between *D. tielianum* and *C. scoticum* in having pinnate cupule segments. The fact that *C. fimbriatum* is basically pinnately branched contrasts strongly with *D. tielianum* where the fertile rachises arise as a direct continuation of the primary rachis.

Walton (1949), in a very full discussion, compared *Calathospermum* with *Gnetopsis elliptica* Renault, *Megatheca thomasii* Andrews, *Calathiops renieri* Walton, and *Calathiops bernhardti* Benson. The first three of these species are only known as detached

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EXPLANATION OF PLATE 45

Figs. 1–7. *Calathospermum fimbriatum* sp. nov. 1, Transverse section of primary rachis containing two dividing C-shaped traces from the extreme base of the cupule; holotype, slide no. G.C. 2296 (peel 3), ×13·5. 2, Transverse section (oblique 30°) of a small detached rachis (*Lyginorachis sp.*?) identical in structure to a primary rachis of *C. fimbriatum* and showing the characteristic broken dentate U-shaped xylem and the bases of two pinnae; G.C. 2378, ×13·5. 3, Transverse section through the holotype showing eight rachises of the central system, together with six rachises of the marginal system surrounded by the cupule segments in various stages of division (compare with text-fig. 1H and I); G.C. 2324, ×3·5. 4, Oblique transverse section showing six segments and centrally two fertile pinna rachises; specimen 6, G.C. 2342, ×3·5. 5, Transverse section of the stalk of an ovule surrounded by hairs (text-fig. 3B); G.C. 2229, ×36. 6, Transverse section through the body of an ovule (text-fig. 3C), showing the crumpled megaspore membrane, superficial layers of integument with five grooves and surrounding hairs; G.C. 2234, ×38. 7, Microspore (?pollen) from lagenostome of small detached ovule; G.C. 2384 (peel 10), ×666.

Fig. 8. *Salpingostoma dasu*, portion of megaspore membrane showing the cellular reticulum on the outer surface; G.C. 2383, ×21.

Figs. 9, 10. *Calathiops sp.* W. Hemingway's photographs of a specimen from Coseley. 9, Specimen in nodule, ×1. 10, Counterpart, ×3.

upules; in the fourth, *Calathiops bernhardti* Benson (1935), the cupules are secund n pinnae which are borne alternately on a major rachis. This is a very distinct type, nd although the cupules appear similar to *C. fimbriatum* the frond bearing them was ery different and probably much larger.

In the M. Benson manuscripts in the British Museum (Natural History) there are me photographs from W. Hemingway, two of which illustrate a compression (specien WH/2356) of what appears to have been a cupule bearing two (? four) ovules. hough it has not been possible to locate the specimen, these photographs are reprouced here as Pl. 45, figs. 9, 10. The specimen was from Coseley, near Dudley, south affordshire (Westphalian B) and was referred by Hemingway to the genus *Gnetopsis*. he cupule is highly divided and ended in at least ten strands though its basal segmentaon is not clear. It closely resembles the cupules of *Calathiops bernhardti*.

More recently Walton (1953) has indicated some features of anatomy and symmetry mmon to *Calathospermum* and some genera of the Trigonocarpales. In the Neuroerids which supposedly bear Trigonocarpalean seeds; the seeds are attached to pinna chises and appear to be morphologically equivalent to pinnules as they are in *Calaospermum*. The cupule of *Calathospermum* appears thus morphologically comparable the vegetative part of a Neuropterid frond and not to the integument of the Trigonorpalean seed. In *Calathiops bernhardti* noted above the cupules seem to be comparable pinnae. A possible explanation is that a transference of cupule function (see Corner 58) may have occurred so that morphologically smaller regions of a frond became volved.

knowledgements. I am indebted to Professor J. H. Taylor for the loan of slides and cut blocks from Gordon collection, to Professor J. Walton for help and advice, to Dr. K. L. Alvin for helpful ticism of the manuscript, to Mr. McGregor for photographic assistance, and to the University of ndon together with the Clothworkers' Company for the William Gilles Research Fellowship ring my tenure of which this work was accomplished.

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P. D. W. BARNARD
Department of Botany,
Birkbeck College,
London, W.C. 1

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THE EXTERNAL ANATOMY OF SOME CARBONIFEROUS 'SCORPIONS'

PART 2

by LEONARD J. WILLS

ABSTRACT. Part 2 is concerned with the anatomy of eight Orthostern 'scorpions', developed by the technique described in Part 1 (*Palaeontology*, **1**, 261–82). Virtually complete skins of two are described. The first is a paratype of *Buthiscorpius buthiformis* (Pocock), the description of which is supplemented from a second, less complete, example. The second is *Mazoniscorpio mazonensis* gen. et sp. nov. Each of the remaining five is incomplete as only half-nodules were available. They comprise a new species of *Buthiscorpius—B. major*; a new genus and species—*Wattisonia coseleyensis*; and three unidentifiable forms. Each provides valuable data about one or more organs: yet there is still no absolutely convincing evidence as to how any of them breathed. There follows a revised diagnosis and description of the Lobostern *Eoscorpius tuberculatus* Peach, here made the type species of *Benniescorpio* gen. nov. The paper ends with a brief discussion of the anatomical and ecological conclusions to be inferred from the descriptions in both Parts, followed by four supplementary notes correcting statements in Part 1 and describing new development-techniques.

INTRODUCTION

THE majority of Carboniferous 'scorpions' have been placed in Pocock's group Orthosterni (see Part 1, p. 267), because a few among them are known to resemble Recent forms in having unlobed parallel-sided sternites. I propose describing here details of the anatomy of eight Orthostern 'scorpions' etched out of ironstone nodules. After the descriptive part, a few general conclusions are stated, but I have made no attempt to revise our knowledge of Carboniferous 'scorpions' in general or to make a critical review of their taxonomy. In fact this last problem can never be successfully achieved until the type specimens have been developed to show details analogous to those achieved by the present etching technique.

I have throughout numbered the segments according to their position on the adult animal: Prosoma, carapace I to VI; Abdomen, mesosomatic VII to XII plus metasomatic XIII; Tail, metasomatic XIV to XVIII plus the sting. According to this scheme the genital operculum lies on the first adult mesosomatic segment (VII); whereas it is generally stated by zoologists to lie on the second mesosomatic (VIIIth) somite of the whole body, since the first (VIIth) or pregenital disappears in embryonic growth 'retaining in the adult only its neuromere, which becomes incorporated in the thoracic ganglionic mass as the 6th pair of its ganglia'. . . . 'The original number (12) of abdominal segments is restored in the course of embryological development by sub-segmentation of the 8th embryonic segment' (Petrunkevitch 1955, p. P68). Presumably Carboniferous 'scorpions' behaved in the same way, but there is, of course, no evidence. See also Størmer 1955, pp. P1, P6, re segmentation in Chelicerata in general and Merostomata in particular.

Repositories. B.M., British Museum (Natural History); B.U., Birmingham University, Geology Department; G.S.M., Geological Survey Museum, London; G.S.E., Geological Survey, Edinburgh; M.M., Manchester Museum.

[Palaeontology, Vol. 3, Part 3, 1960, pp. 276–332, pls. 46–57.]

List of abbreviations used in the illustrations. acl, anterior claw; *acs*, aculeus of sting; *app*, anterior plate of sternum of pecten; *ats*, anterior tarsal spur; *ap*, anterior process of carapace; *avn*, anterior V-notch of sternite; *b*, boss on rachis of pecten; *bch*, basal joint of chelicera; *bo*, border; *C* xiv–xviii, caudal rings of adult segments xiv–xviii; *c* 1–4, coxae of legs 1–4; *ca*, carapace; *ch*, chelicera; *cl*, claw; *cll*, claw-lobe; *cp*, coxa of pedipalp; *cr*, cephalic region of carapace; *d*, dagger; *ebc*, end of broken claw; *et*. eye tubercle; *f*, fulcra; f1–4, femur of legs 1–4; *fp*, femur of pedipalp; *frf*, free fingers; *go*, genital operculum; *gs*, pad or *Gehstachel*; *gr*, granule; *h*, hair; *hch*, hand of chelicera; *hpd*, hand of pedipalp; L. left; L.L. 1–4, left legs 1–4; *lm*, lamella of pecten; *lo*, lobe on metatarsus; *md*, mandibular process of coxa 1 or 2; *me*, median eye; *mg*, median groove of carapace; *mt*, metatarsus; *mts*, metatarsal spur (arising from base of metatarsus); *pa*, patella; *pa* 1–4, patella of legs 1–4; *pap*, patella of pedipalp; *pcg*, posterior cephalic groove; *pcl*, posterior claw; *pd*, pedipalp; *pe*, pecten; *pgs*, poison-gland of sting; *ppp*, posterior plate of sternum of pecten; *ps*, platform spine; *pts*, posterior tarsal spur; *pvn*, posterior V-notch of sternite; R, right; *Rch*, right chelicera; R.L. 1–4, right legs 1–4; *ra*, rachis of pecten; S ix–xii, sternites of adult segments ix–xii; Sxiii, sternal plate of adult segment xiii; *se*, spinule on doublure of sternite; *set*, seta, bristle, movable hair; *sf*, sensory field; *sg*, sting; *sk*, stop-knob; *spe*, sternum of pecten; *spi*, spine; *st*, sternum of prosoma; Tvii–xii, tergites of adult segments vii–xii; Txiii, tergal plate of adult segment xiii; *ta*, tarsus; *tas*, tarsal spur; *th*, teeth of pecten; *ti*, tibia; *tr*, thoracic region of carapace; *tr* 1–4, trochanter of legs 1–4; *tri*, sensory hair-bases (trichobothria); *trp*, trochanter of pedipalp.

SECTION A—ALMOST COMPLETE EXOSKELETONS

ORTHOSTERNI Pocock 1911

BUTHISCORPIUS Petrunkevitch 1953

Buthiscorpius buthiformis (Pocock)

Plates 46–48; text-figs. 1–9

Anthracoscorpius buthiformis Pocock 1911, pp. 24–28, pl. 1, fig. 2, pl. 2, fig. 1, text-figs. 6–8.
Eoscorpius buthiformis Petrunkevitch 1913, p. 35.
Eoscorpius buthiformis Petrunkevitch 1949, pp. 152–3.
Buthiscorpius buthiformis Petrunkevitch 1953, pp. 26, 32, figs. 31–34, 122.

Material. (i) Holotype, B.M. In.18596, Middle Coal Measures, Sparth Bottoms, Rochdale, Lancs. Pocock 1911, pl. 11, fig. 1, text-fig. 6; Petrunkevitch 1953, figs. 31–33, 122. (ii) Paratypes in British Museum, all from Coal Measures, Coseley, S. Staffs.: (1) In.31262, Pocock 1911, pl. 1, fig. 2*a* (here redescribed). (2) In.22832, Pocock 1911, text-fig. 8. (3) In.1555, Pocock 1911, pl. 1, fig. 2. (4, 5) Two specimens in Mr. Egginton's collection cited by Pocock 1911, p. 27 (present whereabouts unknown). One specimen, B.M. In.7883, figured as a paratype by Pocock (1911, text-fig. 7) has been made into the holotype of *Compsoscorpius elegans* Petr. (iii) Other material: B.U.720 (here described).

Remarks. In 1913, and again in 1949, Petrunkevitch assigned *Anthracoscorpio buthiformis* Pocock to the genus *Eoscorpius* Meek and Worthen, but in 1953 he erected *Buthiscorpius* for Pocock's holotype and all but one of his paratypes. Dr. E. I. White, with the sanction of the Trustees of the British Museum, has allowed me to develop both halves of one of the paratypes (B.M. In.31262) with the primary aim of discovering how a typical Orthostern 'scorpion' breathed. Unfortunately only negative evidence on this point has emerged. Each half is now encased in a transparent block of Marco, save for the two pedipalp hands, fragments of legs and comb, and part of the sting which are mounted as micro-slides.

The results of the development confirm Pocock's view that this specimen is conspecific with the holotype of his '*Anthracoscorpio*' *buthiformis*. As regards the generic identification it is best, in my opinion, to use Petrunkevitch's genus *Buthiscorpius* at present, pending a revision of the generic diagnoses of *Anthracoscorpio* Kusta (1884) and *Eoscorpius* Meek and Worthen (1868), on which also awaits the diagnosis of the Family Eoscorpioniidae to which undoubtedly all three genera belong. It may well prove impossible to distinguish the three genera, in which case *Eoscorpius* has priority over the other names.

Revised diagnosis, based on B.M. In.31262 and B.U.720. To the original diagnosis (Pocock 1911, p. 24) with additions by Petrunkevitch (1953, p. 32) can be added: Last caudal ring very long (one-third of whole metasoma), poison capsule rather small and probably somewhat shorter than 6th caudal ring. Sternum and coxae of the legs as described by Pocock in B.M. I.1555, with coxae 3 and 4 fused throughout the length of coxa 3. Genital operculum small. All legs with two claws and two tarsal spurs, and 3rd and 4th legs each with one large metatarsal spur. Pecten probably small. Sternites IX to XII unlobed, overlapping one another briefly and devoid of pulmonary stigmata.

Description of paratype, B.M. In.31262 (Pl. 46, 47; text-figs. 1–5)

Remarks. This specimen was collected by Egginton from the Coal Measures at Coseley, South Staffordshire. It was figured by Pocock (1911, pl. 1, fig. 2*a*) as a paratype of *A. buthiformis*, the figure incorporating data from both halves of the nodule and showing the chelicera more clearly than does the specimen.

As received the specimen lay in two halves of a nodule. One, now numbered In.31262A (and hereafter referred to as A), showed dorsal features seen from the ventral side with Right side elements appearing on the left (Pl. 46, fig. 1)—Pocock's pl. 1, fig. 2*a*, is reversed. On A a thin sliver of stone defined by a crack passing almost parallel to the surface and visible in the photo had been stuck on with shellac. I dissolved this and repaired with 'Seccotine'. The crack had severed the Right appendages which consequently broke away during the etching. The other half nodule, In.31262B, showed ventral features seen in dorsal aspect (Pl. 47, fig. 1). In both halves a good deal of very tenuous chitin was preserved, but in some places the surfaces were casts of the outside of the skin. This arrangement implies that when the nodule was split open the fracture passed between the dorsal and ventral skins, and that any intervening film of matrix was lost, for the dorsal features of A do not appear on B, and vice versa; e.g. the carapace is seen on A and the sternum and coxae on B.

There was no kaolinite reinforcement and only a very little iron pyrites, and the chitin proved to be very thin, transparent, and fragile. Consequently the mounted preparations are disappointingly fragmentary except in one or two cases.

After etching, the exterior of the dorsal surface (minus the sting) was displayed, the skin being preserved in places where it had escaped destruction on the original surface of fracture of the nodule (Pl. 46, fig. 2).

Approximate measurements in mm. Length of carapace, 3·5; abdomen, 8·5; tail, 11; sting, *c.* 4; total, 27.

The *carapace* is damaged at the forward end, but it can be seen that the sides converge slightly towards the front where the antero-lateral corners are rounded and united by a

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EXPLANATION OF PLATE 46

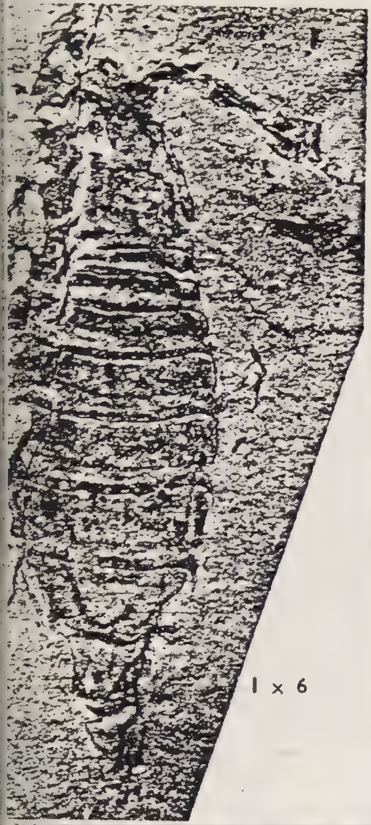
Figs. 1–5. *Buthiscorpius buthiformis* (Pocock), B.M. In.31262A and B. 1, Ventral view of the dorsal surface of A, as received. ×6. 2, Dorsal view of the dorsal surface of A, after development. ×6. 3, Dorsal view of the sting, Slide B.M. In.31262A/2, at about the same magnification as fig. 2. ×7·5. 4, Ditto. ×22·5 to compare with text-fig. 2. 5, Tip of the rachis of the comb with three teeth, each with a narrow sensory field. Slide B.M. In.31262B/11. ×60.

EXPLANATION OF PLATE 47

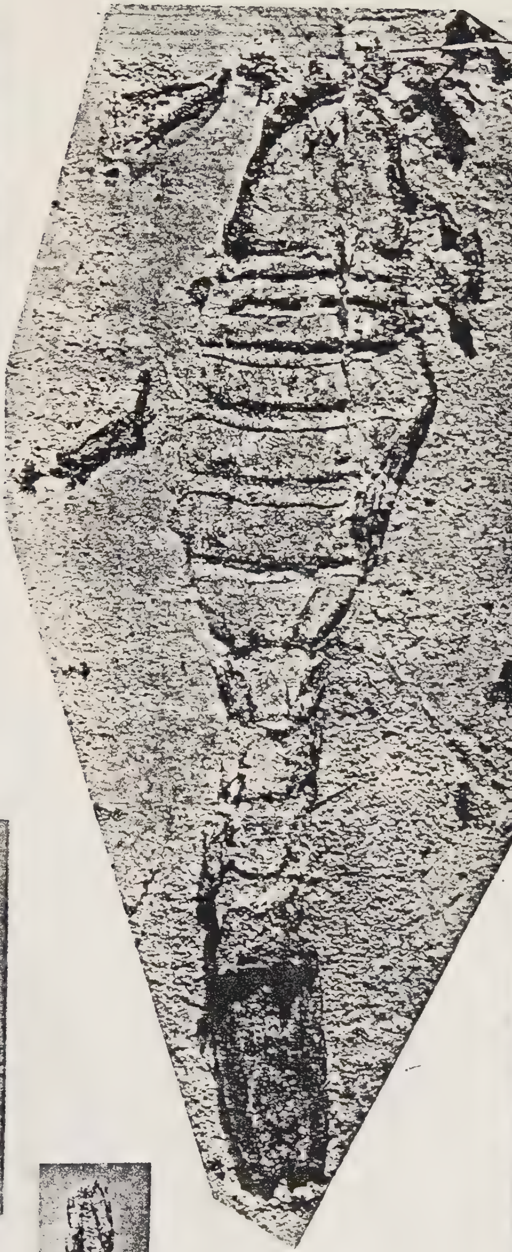
Figs. 1–6. *Buthiscorpius buthiformis* (Pocock), B.M. In.31262A, B. 1, Dorsal view of the ventral surface of specimen B, as received. ×6. 2, Ventral view of the ventral surface of specimen B after development. ×6. 3, Femur, patella, and hand of R. pedipalp. Slide A/1. ×15. 4, Tibia, metatarsus, tarsus, and claws of 1st or 2nd L. leg. Slide B/4. ×15. 5, Part of metatarsus, tarsus, and claws of 1st or 2nd R. leg. Slide B/1. ×15. 6, Metatarsus, tarsus, and one surviving claw of ? 3rd L. leg. Slide B/3. ×15.

For key to abbreviations see p. 277.

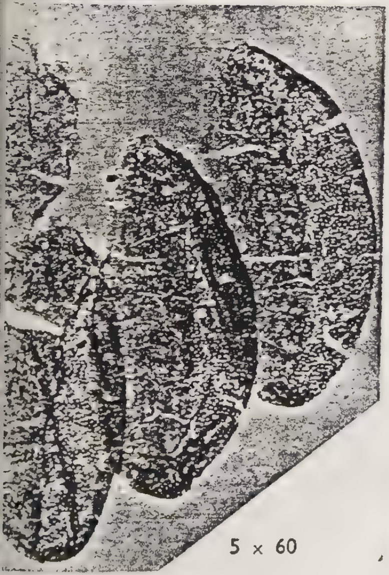
PLATE 46



1 × 6

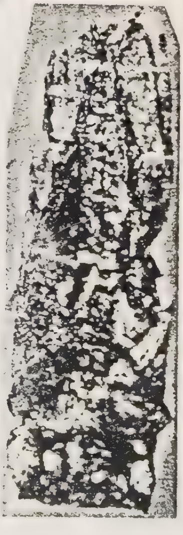


2 × 6

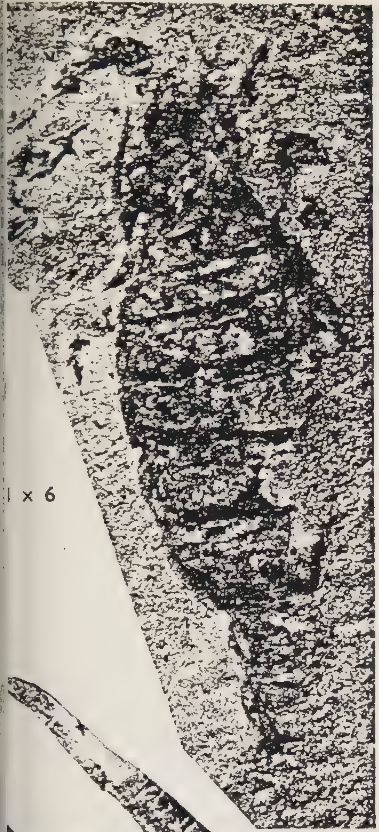


5 × 60

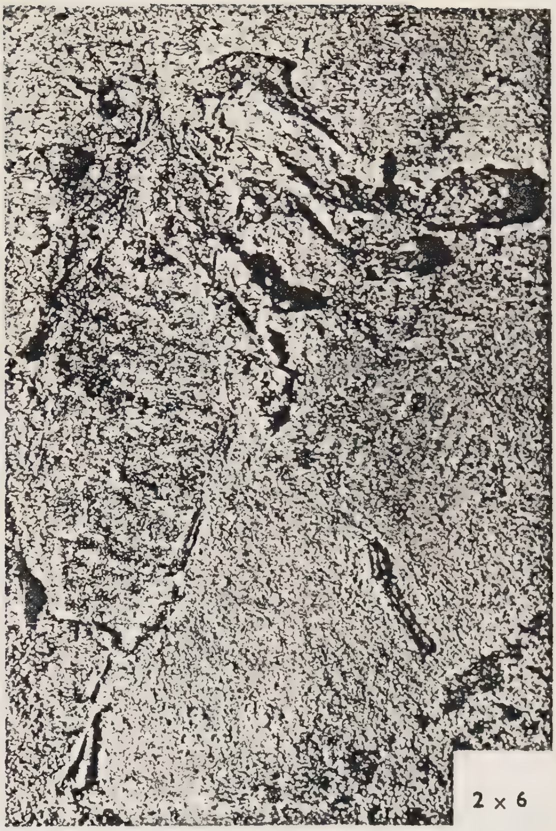
3 × 7·5



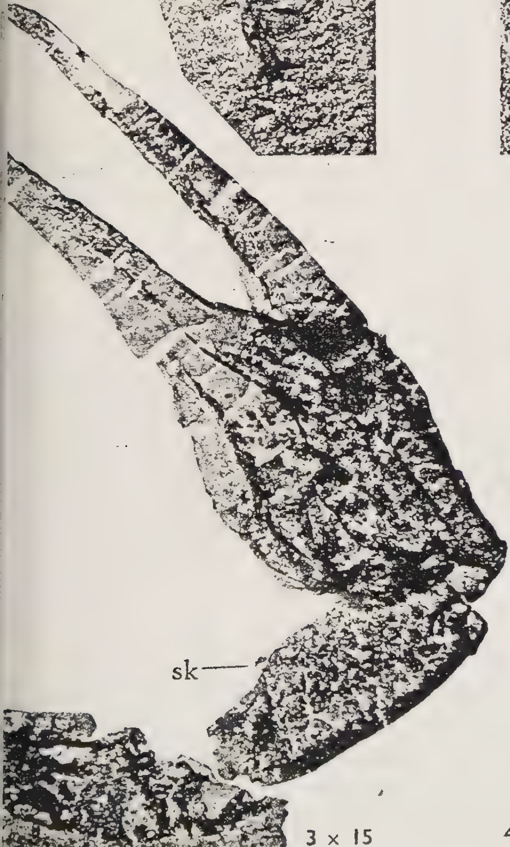
4 × 22·5



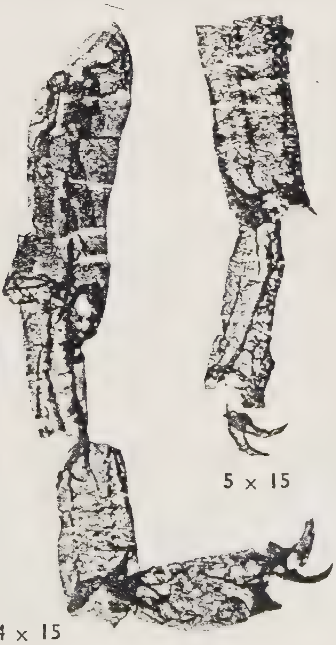
1 × 6



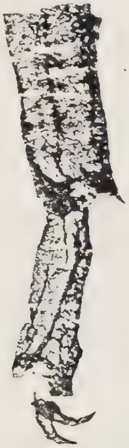
2 × 6



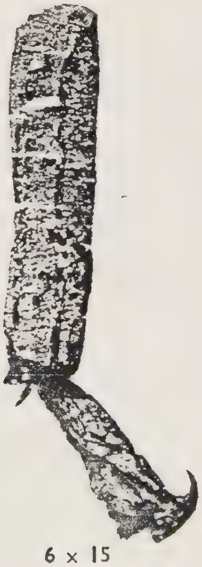
3 × 15



4 × 15



5 × 15



6 × 15

urved anterior margin. The shield is somewhat arched, with a shallow median furrow hat is blocked in front by the ocular tubercle which is situated about one-quarter of the ength of the carapace from the front. The eyes are conspicuous (text-fig. 1): each appears o be a hemisphere with its polar axis pointing almost vertically. As Petrunkevitch 1953, p. 32) states, 'the space between the eyes is elevated'. This elevation is defined by pair of small ridges separated by a median groove. On the right side of the carapace

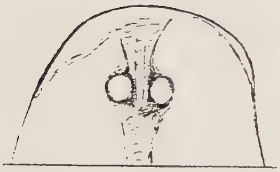


FIG. 1

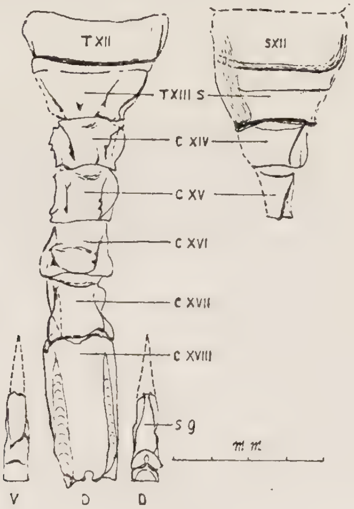


FIG. 2

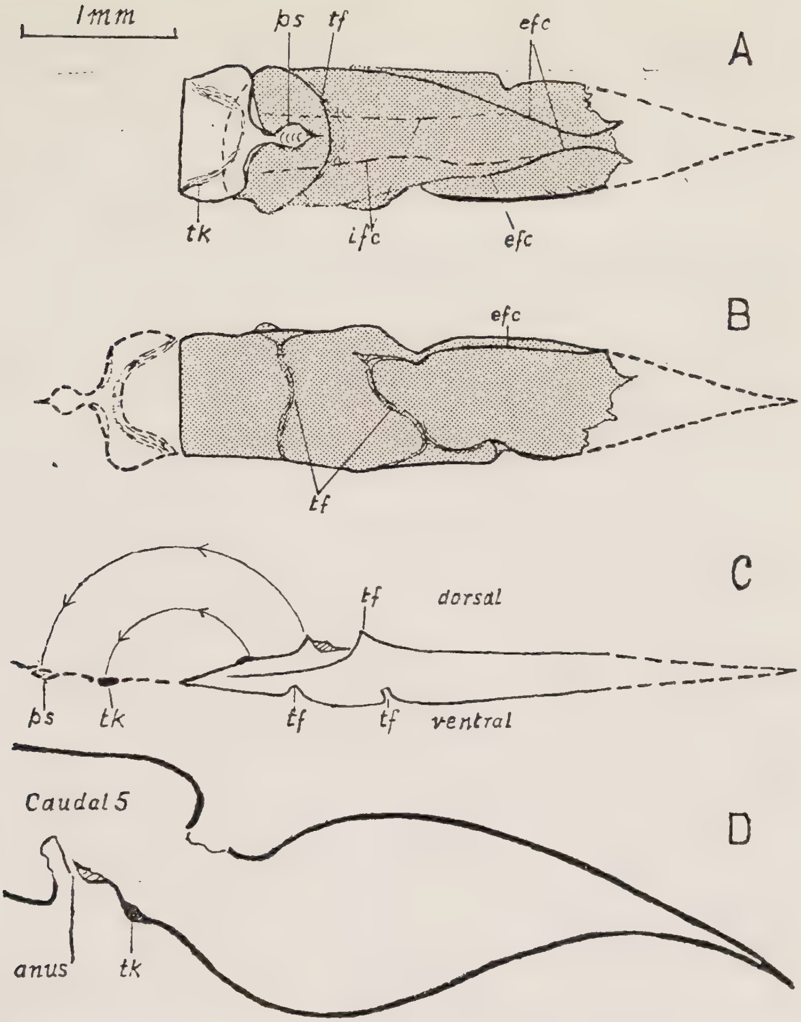
EXT-FIG. 1. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262A, after development. Front half of rapace to show the eye-tubercle with large median eyes separated by two diverging ridges and a narrow median groove. Behind the tubercle is the front end of the median furrow. × *c.* 10.

XT-FIG. 2. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262A. Dorsal view of the metasomatic segments and sting. For key to abbreviations see p. 277.

e antero-lateral corner is fairly well preserved and shows no lateral eye ridges or lateral celli. The posterior margin is mucronate and passes into linear lateral margins. No rnamentation can be seen.

The *mesosomatic tergites* are quite normal, being very short in the front of the body d increasing in length so that tergite XII is at least twice as long as tergite VII. The idth increases from tergite VII to tergite X, and then remains almost constant back to e articulation of tergite XII with the tergal plate XIII. The posterior margins are defined y lines of granular and mucronate tubercles, the anterior margins are linear. Wide rips of intersegmental skin are exposed, showing that the animal was entombed in a istended state.

The *metasomatic segments.* The dorsal surfaces of all the metasomatic segments ched out perfectly (Pl. 46, fig. 2), the end of the tail floating free in the acid (it now lies ee in the Marco block, text-fig. 2); but only certain parts of the ventral surface of the il can be examined, for it proved impossible to remove all the matrix from below the ee-floating end in A, and only the skin of the 1st and of parts of the 2nd and 3rd etasomatic segments is preserved in B (text-fig. 2). The shapes and relative proportions



TEXT-FIG. 3. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262B/2. The poison-capsule with the missing aculeus restored (broken line). A, Dorsal view of dorsal skin (stippled) and of inverted proximal process of the ventral skin (unstippled) with semi-annular thickening, *tk*, and ? periproctal skin, *ps*; transverse fold, *tr*; external and internal fold-crests, *efc*, *ifc*. B, Ventral view of ventral skin (stippled) with its proximal process (unstippled) restored to its original position. C, Sagittal section of specimen with its proximal part (broken line) restored as in B. D, Tentative restoration of the poison-capsule in relation to caudal ring 5 and the anus, in sagittal section.

of the metasomatic segments are fairly normal, the first four all having much the same length, the fifth being somewhat longer and the sixth (perhaps abnormally long) being about three times the length of the first. The first (Txiii) has the usual sharp taper backwards from the full width of the body to the narrow width of the caudal rings (the latter have been flattened and appear wider than they originally were). The whole segment consists of a dorsal and a ventral plate united by a wedge of pleural skin. The two plates taper sharply backwards to articulate with the first caudal ring. With the wedge

of pleural skin they resemble a pair of old-style bellows. The sides of each plate are defined by marginal ridges which unite in blunt spines at the apex of each pleural wedge. On the dorsal plate there are also two sharp keels ending in formidable thorns, and a strong median spine. Both plates have linear anterior margins, that on the ventral plate lying much farther back than that on the dorsal, and with a correspondingly broader anterior border of intersegmental skin (possibly an adaption to the habit of inverting the tail over the animal's back).

Caudal rings xiv–xvi each have a pair of dorsal keels armed with spinelets and ending in a large thorn like those on Txiii. In Cxvii and Cxviii the corresponding keels are wider, flatter, and free from spinelets and thorns.

Owing to flattening and to the obscuring by matrix, details of the sides and ventral surfaces of the caudal rings cannot be completely elucidated, but probably ventrolateral keels marked the limits of the lower surface of each ring. The keels end in rather lat angular processes which are progressively larger as the end of the tail is approached, he pair on the last caudal ring being conspicuous and separated by a sinus, behind which the anus would lie.

The sting. The poison capsule lay symmetrically inverted over Cxviii. Unfortunately he aculeus itself was missing, probably as a result of my having ground away the back f the nodule a tiny fraction too much, the cut removing the dorsally projecting point f the sting. The rest of it, about 3 mm. long, etched out complete (Pl. 46, figs. 3, 4; ext-fig. 3) as an almost cylindrical object. It is not absolutely certain which of its suraces is the ventral one that, being inverted over Cxviii, was first laid bare by the etch, ut the supposed dorsal side lies upwards on Slide A/2. Being quite transparent it can e examined from both sides and by reflected or transmitted light. The originally ask-shaped capsule was not flattened in fossilization, but was partially collapsed in a emarkably symmetrical way by the flexing of its curved sides inwards in two large and wo small longitudinal folds, and transversely by one deep fold on the dorsal, and y two lesser ones on the ventral side; and the median proximal process on the ventral de was inverted so that its end pointed distally, text-fig. 3a, b, c. This process ends in triangular piece that continues into thin plates which may be remains of the skin and muscles lying near the anus and connecting the sting to the last caudal ring.

Taking account of the inversion of the process, and the positions and sizes of the nfolds (which can be traced out within the transparent sclerite), it seems likely that the capsule bulged dorsally and laterally near its proximal end, and that it had shallow ateral grooves (as occur in some Recent forms) which determined the position of the wo conspicuous deep longitudinal infolds. On text-fig. 3d I have attempted a reconstruction of the actual sting as it would have appeared in sagittal section.

Organs of the ventral surface (text-fig. 4)

The original fracture that split open the nodule passed through the chelicerae and the basal parts of the pedipalp, and then between the carapace and the inside of the coxae of he legs and the sternum. In the mesosoma it passed between the tergites and the ventral rgans (genital operculum, the sternum of the pecten and the four sternites). As a result he chelicerae and the coxae of the pedipalp were much damaged, and most of the two combs were lost. The etching of specimen B, however, revealed the outside or ventral urface of the coxo-sternal area and of the mesosomatic ventral organs in fair detail.

Chelicera. Only part of the hand of the chelicera shows in specimen A (Pl. 46, fig. 2, *ch*). It appears to be of normal proportions.

Pedipalp. Apart from the coxae, both pedipalps are fairly well displayed, and the hands were both extracted (Slide A/1, Pl. 47, fig. 3, and Slide B/2). The R. coxa is probably visible where it projects beyond the side of the carapace in A; the left one is seen in B to lie dorsally to the coxa of the 1st leg, but its shape is difficult to make out. The trochanter, femur, and patella are quite normal, the L. femur showing the row of granules noted by Pocock—'the femur of the left chela with an anterior granular crest, such as is present in most recent scorpions'. The whole of the R. patella (*pap*) is preserved in Slide A/1 (Pl. 47, fig. 3). It shows a 'stop knob' (see p. 304) on its anterior side and traces of small granules. Owing to crushing the original shape of the hand (*hpd*) is hard to determine, but the palm must have been stouter than the present outline would suggest. The fingers are somewhat longer than the palm and they taper gradually, to end in points slightly hooked towards each other. The biting edges are a little thickened, but devoid of granules. Under a high power of the microscope minute hair-bases, some perhaps trichobothria, can be seen near the tips and elsewhere.

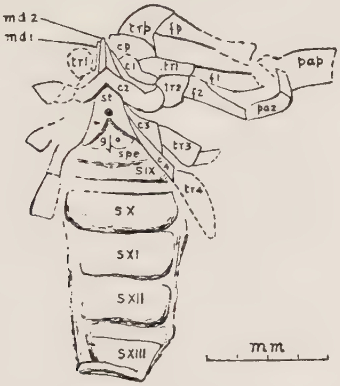


FIG. 4

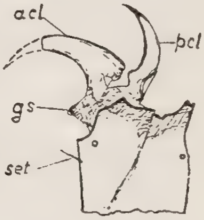


FIG. 5

TEXT-FIG. 4. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262B. Ventral surface of body after development. Cf. Pl. 47, fig. 2. For key to abbreviations see p. 277.

TEXT-FIG. 5. *Buthiscorpius buthiformis* (Pocock). B.M. In.31262B/4. Claws and end of tarsus (in posterior view) of ? 2nd L. leg. Cf. Pl. 46, fig. 11. × *c.* 60. For key to abbreviations see p. 277.

In general the whole hand resembles that extracted from *B. major* sp. nov. (G.S.M. Za. 2926, Pl. 52, figs. 1, 2); but is relatively more massive and with shorter fingers. The whole pedipalp was large and massive in proportion to the legs.

Sternum of the prosoma (*st*) is six-sided, but is best described as pentagonal with the posterior side deeply excised, as a result of which the sclerite resembles a bluntly tanged arrowhead. Near the apex of the excavation there is a deep pit with its bottom pointing backwards. The sternum therefore agrees closely with Pocock's drawing (his pl. 1, fig. 2) of the ventral aspect of the coxo-sternal area of one of his paratypes (B.M. I.1555). Along the left side coxae 3 and 4 (*c* 3, 4) can be seen to abut against it, coxa 4 being much longer than coxa 3, and stretching back almost to the 2nd sternite. The two seem to be fused throughout the part in which they are adjacent to one another, as are the

orresponding articles in Recent scorpions. This is an important observation, confirmed y what is seen in B.U. 720 (p. 288), because it negatives one of Petrunkevitch's tentative iagnostic characteristics of Eoscorpiidae—coxae of 3rd and 4th pairs of legs 'probably ot yet grown together along their line of contact, retaining independent motion' (1955, . P73), and shows that in the present genus at any rate the coxal arrangement was in his respect the same as it is today. Coxae 1 and 2 also conform exactly to the pattern ound in Recent scorpions. The mandibular processes are well displayed, those on coxa 2 eing the larger and lying side by side on the middle line. The other articles of the four egs are minute and their skin is so tenuous and devoid of any reinforcement that claws, purs, and even individual joints were inevitably detached during the etching. Though everal parts were recovered and mounted as Slides A/3–A/8 and B/1, B/3–B/8, it was mpossible in some cases to be certain about their individual provenance, nor can one be ertain that the surviving claws and spurs represent the original full complement. For hese reasons only approximate estimates of the lengths of the appendages can be made. ee Table, p. 289. The parts recovered (a few of which are illustrated on Pl. 47, figs. –6) do, however, compare so closely in shape or structure with the better preserved xamples in B.U. 720 (Pl. 48, fig. 6; text-fig. 6) that it may be safely assumed that these mbs were organized on the same pattern. The detailed structure of the claws with their ad (*Gehstachel*) can be seen in Slide B/4 (text-fig. 5). No denticles can be seen on the laws, a feature possibly related to the small size of the individual.

esosoma. The *genital operculum* (*go*) is small, its two halves filling the posterior sinus f the sternum. The left half has been pushed under the right half far enough to damage nd displace the median edges of both.

The *sternum of the pecten* (*spe*) appears to be short and possibly bilobed, but no details re visible. Remains of both combs were seen, but only a few teeth were recovered Slides 10–12, Pl. 46, fig. 5). Each is a flattened sack, pointed at its proximal end and ounded distally, with a narrow sensory field thickly covered by peg-organs (Part 1, . 274). The field occupies a lanceolate strip running from end to end. This arrangement s probably the normal one in Carboniferous 'scorpions', but the example here photoraphed reveals it more clearly than any of the other specimens so far found. What I aw of the combs suggested that each was short, with teeth few in number and attached o a narrow slight rachis—the whole resembling the comb of a Recent scorpion more han the fan-like ones found in *Lichnophthalmus*, *Pareobuthus* (Part 1), and *Benniecorpio tuberculatus* (Peach) (below).

The *sternites of adult segments* IX–XII, exposed on the original ventral half nodule (B) ut not noticed by Pocock, revealed disappointingly meagre details after etching, probbly because the ventral skin was extremely thin, crushed against the dorsal, and amaged when the nodule was split open. Sternite IX was better seen on the surface riginally exposed (Pl. 47, fig. 1) than it is now after etching. It is short and ill-defined in ront where it may have merged into the sternum of the pecten with but little marginal hickening of either sclerite. The others are much of a size, each about one-third longer han sternite IX. Each agrees roughly in length with its corresponding tergite. Traces of inear anterior margins can be seen here and there. The posterior margins are unrnamented, but appear dark, mainly as the result of the infolding of the intersegmental kin in a deep doublure. It is this belt of overlap that showed up as a broad stripe

between adjacent sternites on the internal surface as originally exposed (Pl. 47, fig. 1). The postero-lateral angles of sternites X–XII are rounded and clearly overhang (in ventral aspect) the pleural skin which here merges with the infolded intersegmental skin. There is no sign of any stigmata on any of the sternites or on the pleural or infolded intersegmental skin; nor can I detect any minute hairs or spinules on the infolded skin such as occur in *Pareobuthus* and *Lichnophthalmus* (Part 1). The depth of the intersegmental infold where one sternite overlaps the next one behind, although about one-third of the length of the sternite, would appear to be too small for an adequate cover to gills: how this animal breathed remains a mystery.

Description of B.U.720 (Pl. 48; text-figs. 6–9)

Remarks. This specimen appears to resemble the paratype of *B. buthiformis* just described (B.M. In.31262) so closely that it may confidently be referred to the same species. In particular it agrees in regard to dimensions and proportions, the shape of the carapace, the position of the median eyes, the apparent absence of lateral eyes, and in the organization of the coxo-sternal area. However, the front end of the carapace is not well preserved, and there are features towards its antero-lateral corners that in some lightings might be interpreted as lateral eyes. Were these certainly present the specimen would have to be referred to *Compsoscorpius* Petr., one species of which, *C. elegans* Petr., is based on another of Pocock's paratypes of *Anthracoscorpio buthiformis* (B.M. In.7883). The Birmingham specimen is particularly instructive because its legs were extracted almost intact with spurs, bristles, thorns, and spines still attached—features used extensively in the classification of Recent scorpions.

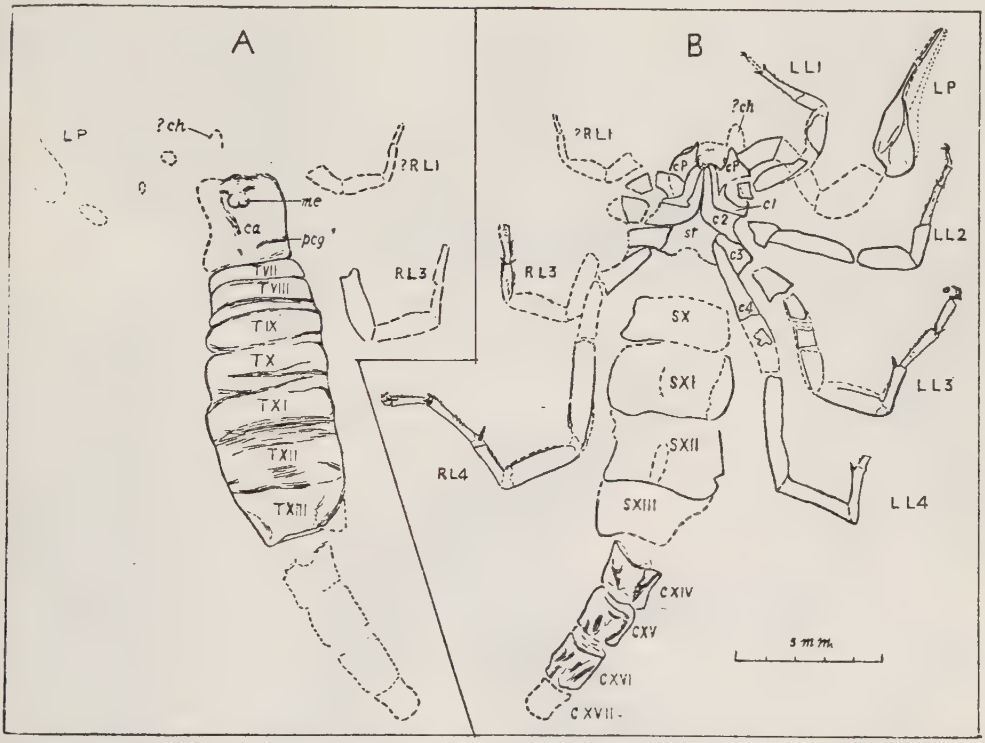
This was the first specimen to which, with Dr. Isles Strachan's help, I applied the embedding and hot-etching technique described in Part 1. The fossil, preserved in one half of a small ironstone nodule of the 'pennystone' type, was found by me many years ago amongst duplicate material of unknown origin in the Geology Department's possession. It had been almost certainly obtained from the Coal Measures of South Staffordshire, probably from above the Thick Coal at Coseley. Impressions of the dorsal surface as originally exposed were made in collodion, plastone, and dental wax, and it was photographed some years ago (Pl. 48, figs. 1, 2). As it was seen that bits of the original chitinous skin were preserved, I attempted to embed it in balsam with a view to etching with HF, but I was not satisfied and I dissolved off the balsam. Nothing further was done until 1956 when we took advantage of the development of the new transparent plastics to embed it in Marco and etched it with hot HCl. As a result, the following organs (some in a broken state) were isolated, and mounted: the sternites, the sternum, and attached coxae of the pedipalp and legs, the trochanter and hand (minus the movable finger) of the pedipalp, the remaining joints of three left legs, and parts of the right legs. In this instance, unlike the preservation in B.M. In.31262, the chitinous skin in some parts had been covered with, and cavities had been filled by, kaolin which functioned to keep the original shape and relief of the various parts even after they had been extracted. Embedded in the kaolin, however, were many bristles which have the appearance of having been torn away from the skin, as described and figured in Part 1 (p. 263; pl. 50, fig. 16), the figure being a photo of the metatarsus of the 3rd leg of the present specimen. At the end of the etching a very good transparent cast was obtained of the originally exposed surface, with a fair amount of chitin fragments embedded in it (Pl. 48, fig. 3).

EXPLANATION OF PLATE 48

Figs. 1–7. *Buthiscorpius buthiformis* (Pocock), B.U.720. 1, Dorsal view of the dorsal skin of the body and of the ventral skin of four caudal rings before development (cf. text-fig. 6A). ×3. 2, Ditto, to show carapace and eye-tubercle. ×5. 3, Dorsal view of Marco-cast after development. ×5. 4, Left pedipalp hand in dorsal view. Slide *k*. ×7½. 5, Ditto, in ventral view. ×7½. 6, Ventral view of ventral organs reassembled in approximately their original relative positions; based on Slides *a*, *b*, *d*, *h* (cf. text-fig. 6B). ×7½. 7, Hairs at the entrance to the mouth, probably on ventral side of the base of the chelicerae. Slide *g*. ×225.

For key to abbreviations see p. 277.

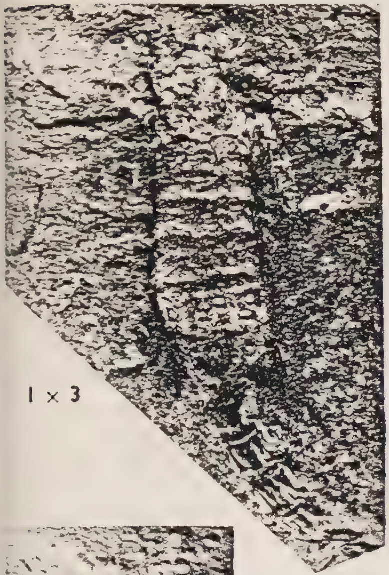
Dimensions. The body was preserved in full relief, and consequently appears narrower in proportion to its length than it would had it been flattened. Approximate measurements and estimates given below agree closely with those of the holotype, of B.M. In.31262, and other paratypes. As scorpions go, these specimens represent either immature individuals or adults of a really small species, probably the latter. *Approximate measurements in mm.* Length of carapace, 3; of abdomen, 9½; of tail (4 segments only), 7½; whole body (estimated), 24–25; greatest width of carapace (apparent), 3·8; of mesosoma (apparent), 4·4; of mesosoma (estimate assuming it were flattened), 6·0. For dimensions of the legs see Table, p. 289.

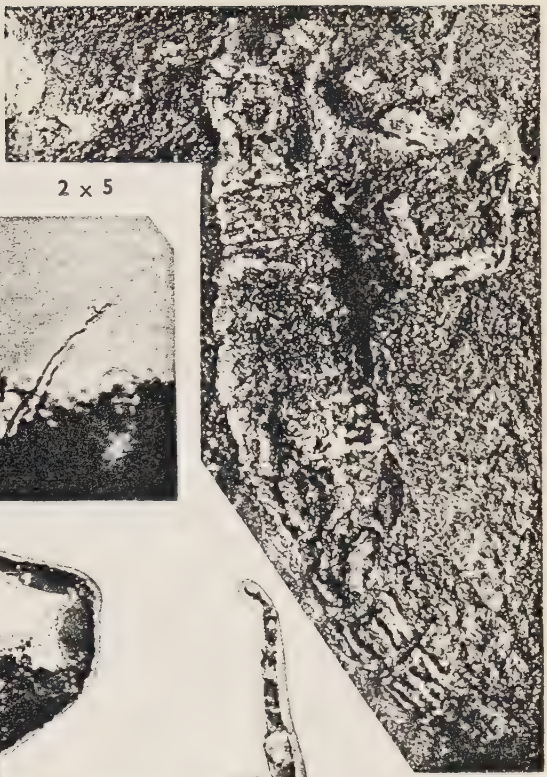


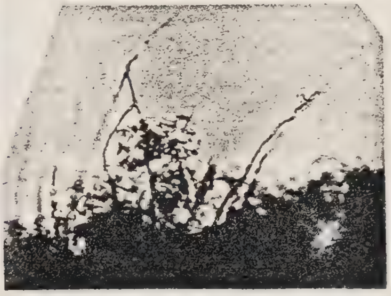
TEXT-FIG. 6. *Buthiscorpius buthiformis* (Pocock). B.U. 720. A, Dorsal view of dorsal sclerites. B, Ventral aspect of ventral parts with appendages restored. Cf. Pl. 48, fig. 6. For key to abbreviations see p. 277.

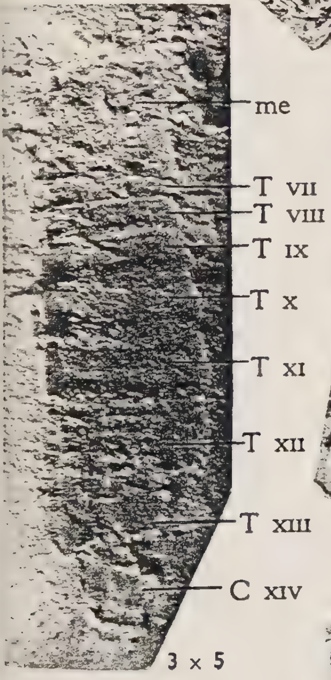
Dorsal features of the body

The *carapace* (Pl. 48, figs. 2, 3; text-fig. 6A) was exposed as a poor internal mould, and practically all the chitin had been lost. It was strongly arched, and before development it appeared to be longer than wide, but afterwards it was seen to be almost square, or wider than long if allowance be made for the arching (compare Pl. 48, figs. 2 and 3). The shape of the damaged anterior margin appears to have been slightly emarginate (as in *Eoscorpius typicus* Petr.). The posterior margin is practically straight. In front of, and parallel to the latter at about one-sixth of the length of the carapace, is a slight transverse post-cephalic groove—a feature frequently found in fossil and Recent scorpions that may perhaps be connected with the attachment of the antero-posterior muscle (Werner 1934, p. 63, figs. 39, 40). (A similar groove in *Proscorpius* and *Palaeophonus* is interpreted by Petrunkevitch as proof that the first tergite was concealed under the carapace and

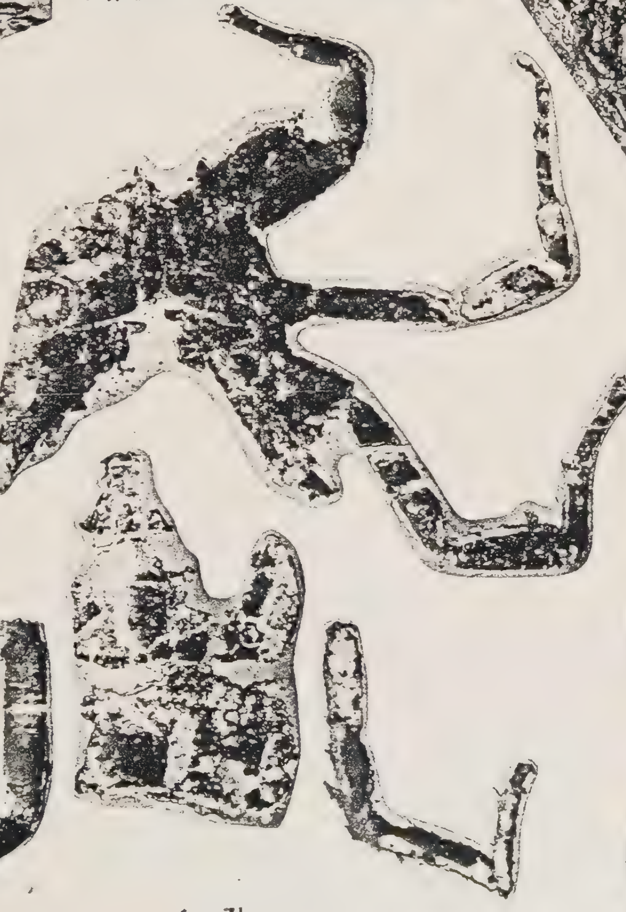

1 × 3


2 × 5


7 × 225



3 × 5



6 × 7½

4 × 7·5

5 × 7·5

that therefore these Silurian forms had seven mesosomatic tergites, not the usual six. This assumption appears to me to be entirely unwarranted, and to introduce a false basis to his classification in Petrunkevitch 1955, p. P69.)

A fairly large eye-tubercle carrying the two median eyes lies about a third of the carapace-length from the anterior margin. It is surrounded by an almost circular depression. The eyes are damaged but appear to lie closer to one another than in B.M. In.31262 and to be without intervening ridges.

The six *mesosomatic tergites* are best seen in Pl. 48, figs. 1, 3, which show them to increase greatly in length from front backwards; but their margins are poorly defined because all the chitin has gone, and we are looking at an internal mould (see text-fig. 6A, TVII–XII). The body was preserved fully distended with the intersegmental skin stretched out between the tergites, giving the impression of great length in relation to breadth. This power of extending the length of the tergum was probably possessed by many Carboniferous 'scorpions'. It, and the misleading appearance that may arise from it, is fully discussed on p. 320.

The dorsal plate of the 1st metasomatic segment (TXIII), poorly preserved, appears to taper unusually slowly. There are no strong keels on it. Possibly part of the sternal plate XIII is to be seen at the right postero-lateral corner.

External casts of the ventral sides of four caudal rings of the tail were originally present (Pl. 48, figs. 1, 2; text-fig. 6A). Partially flattened, they appeared stout and abnormally wide with traces of costal ridges, but the chitin having been lost no details could be seen. During preparation most of the tail was ground away, and now only the first caudal ring can be seen in the Marco-cast (Pl. 48, fig. 3). The fifth ring and the sting were not present in the half nodule.

Appendages and ventral features of the body

The *chelicerae*, originally poorly exposed, now show as casts in the Marco, but no details can be made out and no part was recovered.

The L. *pedipalp* was originally shown up by patches of white kaolin that indicated the presence of the trochanter, femur, patella, and hand, extended in all over a distance of about 7½ mm. Of these joints the L. trochanter, together with L. and R. coxae, were recovered on slide *g* (Pl. 48, fig. 6; text-fig. 6B), and the L. hand, minus the free finger, on Slide *k* (Pl. 48, figs. 4, 5). The L. *coxa* is well seen in slide *g*. It has the normal shape, including the maxillary lobe extending towards the middle line and provided with fine hairs (see below). The *hand* (Pl. 48, figs. 4, 5) is very slender and produced into a rod-like finger. The whole hand measures 5·5 mm. (as compared with 7 mm. in In.31262), made up of about equal lengths of palm and fixed finger. Its maximum breadth is 1·5 mm. On the dorsal inner surface at about one-third of the length from the proximal end is a small but prominent knob, but little else can be seen on this side. On the other, one or two minute hair-bases are visible near the base and tip of the finger (as in *Buthiscorpius major* and *Mazoniscorpio mazonensis*, below), but there is nothing that can be regarded as a row of granules along the biting edge. The free finger was not recovered.

Any differences that may appear to exist between this not completely flattened hand and the crushed examples in B.M. In.31262 (Pl. 47, fig. 3), above, are due to differences in original size and in the mode of preservation. The long slender finger compares well in shape with those figured for several other supposed Eoscorpionids—*Eoscorpius typi-*

cus, *Compsoscorpius*, *Alloscorpius* and *Trigonoscorpius*, and with the Archaeoctonid genus *Eoctonus*; but in all cases the fingers appear more robust than does the one which has survived in this specimen.

The organs around the mouth (text-fig. 7). In Recent scorpions the entrance to the mouth is virtually a hollow tube-like filter formed by the chelicerae and labrum above, by the maxillary lobes of the pedipalpal coxae at the sides, and below by the mandibular processes of the 1st and 2nd legs. All of these may be thickly covered by brushes of forward-directed bristles and hairs, forming a perfect filter to exclude all solids. In the fossilization of the present remarkable fossil, this entrance became filled with ironstone, but after solution of the latter it now appears (on Slide *g*) as an open cavity into which project short fine hairs attached to the chitin of the pedipalpal coxae and to the mandibular processes of the 1st and 2nd legs, and some similar hairs lying in the kaolin and not attached to any visible chitin, but in a position corresponding to the chelicerae and/or labrum (Pl. 48, fig. 7; text-figs. 6B, 7A, B).

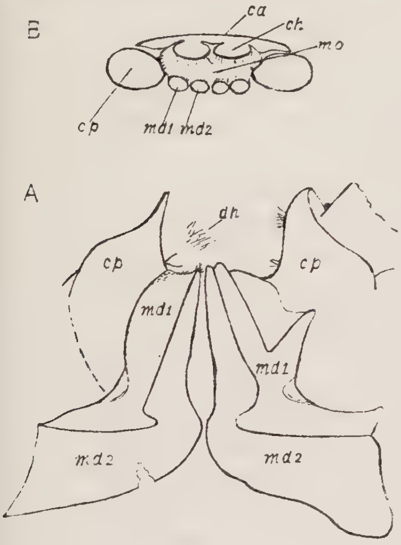


FIG. 7

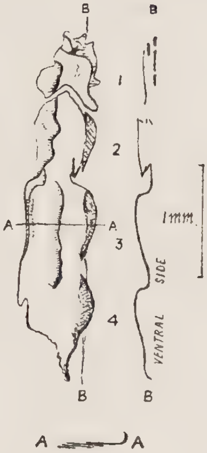


FIG. 8

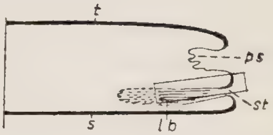


FIG. 9

TEXT-FIG. 7. *Buthiscorpius buthiformis* (Pocock). B.U.720. A, Mouth parts showing hairs attached or (*dh*) detached from the dorsal side of the mouth, now in the kaolin, originally on the chelicerae. Highly enlarged. B, Diagram-section through the mouth (*mo*). For key to other abbreviations see p. 277.

TEXT-FIG. 8. *Buthiscorpius buthiformis* (Pocock). B.U.720/*M*. ? Part of the lung-books—chitinous skin at the pleural ends of four sternites, drawn in dorsal aspect with lighting from right to emphasize the ends of overlapping films of chitin and the blotchy chitin on right (heavy shading); and sections along AA and BB. Cf. text-fig. 9.

TEXT-FIG. 9. *Buthiscorpius buthiformis* (Pocock.) B.U.720/*M*. Hypothetical sections through the right half of a body segment to illustrate the position of Slide /*M* (cf. text-fig. 8), which is outlined by a small rectangle, in relation to a possible pulmonary pouch with a stigma (*st*), a sternite (*s*), and a tergite (*t*); laminate respiratory organ, diagrammatic (*lb*); pleural skin (*ps*).

Taken in conjunction with the hairs actually still attached to the chelicera of *B. major*

was already adapted to moving about easily on land, a feat that *Lichnophthalmus* (Part I) with its stiletto heels could never have achieved.

As in Recent forms, each leg terminated in a pair of non-denticulate curved claws diverging from an angular basal pad. This was well seen in the 3rd L. leg, but the slide (*a*) was subsequently damaged and the part lost in remounting. It agreed exactly with the claw-parts on the 3rd leg of In.31262 (text-fig. 5).

The absence from *B. buthiformis* of the denticles that occur on the claws of all the larger 'scorpions' here described is perhaps to be correlated with the small size of the species.

TABLE

Lengths in mm. of the body, the pedipalp, and legs (exclusive of the claws) of *B. buthiformis*

	Body (less tail)	*Pedipalp arm+hand*	*1st leg*	*2nd leg*	*3rd leg*	*4th leg*
Holotype B.M. In.18596 .	12·1	? 11·5 ? 7·0+4·5	..	..	..	..
Paratype B.M. In.31262 .	12·5	14·5 8·0+6·5	? *c.* 7–8	? *c.* 8	? *c.* 9	*c.* 15
B.U.720	12·5	*c.* 12 ?6·5+5·5	8·2	11·3	13·3	16

The three distal articles (tarsus, metatarsus, and tibia) of each leg carried a variety of immovable spines and spinelets on keels, crests, and round their distal ends, together with movable hairs, thorns, and bristles (some ? trichobothria); but the three proximal ones (patella, femur, and trochanter) are, like the coxae, virtually devoid of any such. Of considerable interest is the occurrence of two *tarsal spurs* sited on the skin between the tarsus and metatarsus of each leg and of one *metatarsal* spur on the skin between the metatarsus and tibia of the 3rd and 4th legs (these names for the spurs have been adopted here as indicating the positions on the leg, whereas the terms 'tarsal spur' of English authors and 'Grunddorn' and 'Tarsalsporn' of Werner 1934, p. 35, do not). Now, in the classification of Recent scorpions the number and distribution of such spurs are characteristics of a whole genus or even a family. When I later developed *Mazoniscorpio* I found the number and distribution of spurs to be just as in the present case, and I suspect that the same is true for all the Orthostern Carboniferous 'scorpions'. Further, it is most remarkable that this arrangement can be matched exactly in Recent scorpions, but only in members of one family—the Buthidae.

The distribution of fixed spines, movable hairs, and bristles on each of the three distal articles of the legs can be epitomized as follows:

Tarsus with some small rather blunt bristles (? rudimentary thorns or *Dornen* of Werner), especially a large group on the distal half of leg 3.

Metatarsus with two rows of short bristles on legs 1–3, scattered bristles on 4, a distal group of bristles on 3 and 4. Two rows of short spinelets on 2 and 3, but none on 1 and 4. One end-spine on all legs.

Tibia with no rows of bristles, but a few scattered ones at the distal end on legs 2, 4, and ? 3.

A few small but conspicuous hair-bases can be seen on the tarsus of legs 3 and 4, on the metatarsus of all four, and on the tibia of legs 1–3. These may perhaps be regarded as the thecae of slender sensory

hairs (? trichobothria), because in no case has a bristle survived in attachment to them, whereas there are many short bristles to be seen (above) which do not appear to spring from any definite hair-bases. It is interesting to note that among Recent scorpions trichobothria are not known to occur on the legs except in immature individuals.

The *genital operculum* and *pecten* were missing.

The *sternites*. Scraps of sternites I and II are mounted on Slides *l* and *n*, part of sternite II and most of III and IV on Slide *h*; and on slide *m* bits of them which were extracted from the pleural region between the sternites and tergites. The chitin of the sternites is very thin and devoid of ornament, hairs, and hair-bases, except for the minutest of prickles and hair-bases on the posterior and postero-lateral margins (Slides *h* and *l*). Sternites III and IV are roughly rectangular, slightly wider than long, with the postero-lateral corners rounded and posterior margin slightly emarginate. In Slide *n* this edge can be seen to be double for a very short distance forward, suggesting that one sternite overlapped the next behind, but the preservation is not good enough to allow us to determine the extent of overlap or to see whether or not there are pulmonary stigmata on the postero-lateral border, where they occur in the Triassic scorpion *Mesophonus* (Wills 1947); but it can be stated definitely that there are no stigmata on the external surface of any of the four sternites, so far as they are preserved (and this covers the greater part of sternites III and IV).

On Slide *m* was mounted a part of the pleural intersegmental area lying between the tergites and sternites. It is sketched in supposed dorsal aspect on text-fig. 8. On it there are four narrow strips of chitin (1–4) lying lengthwise along one side. They are somewhat blotchy, and darker and less transparent than the rest, and may represent the skin originally dorsal to the ends of the sternites. Nos. 2–4 stand up at right angles to the general plane of the specimen which seems to consist of two or three sheets of excessively thin chitin, the top sheet being continuous with the upturned part of No. 3 (see section A–A on the text-figure). I find it impossible to interpret the specimen with any degree of certainty, but I am inclined to regard what I have sketched (it lies upward on Slide *m*) as possibly respiratory structures originally lying dorsal to the R. ends of the four sternites, the shortest (top of figure) being the most anterior. If this hypothesis is correct, it would suggest that a pulmonary pouch and stigma existed between the external end of each sternite and the corresponding dark strip which was part of the pleural skin, and that in this pouch lay the thin chitinous laminae, forming some kind of lung-book. This speculative explanation is shown in text-fig. 9.

MAZONISCORPIO gen. nov.

Type species *M. mazonensis* sp. nov.

Mazoniscorpio mazonensis sp. nov.

Plates 49, 50, and 51, figs. 4–6; text-figs. 10–13

Holotype. B.U.721A, B, and C. Pennsylvanian, Mazon Creek, Illinois.

Remarks. The holotype is on permanent loan to the Geology Department, Birmingham University, from the Botany Department, University of Illinois, Urbana. The large nodule had been split in two roughly on the plane of the dorsal skin. The half labelled A originally displayed dorsal features seen in ventral view (Pl. 49, fig. 1) with grooves on the carapace appearing as ridges. After development it showed the external aspect of the dorsal skin (Pl. 49, fig. 2) except where that had been lost. Here it

presented a mould of the inside of that skin on the Marco-cast. This has now been filled in and become a transparent Marco-block, 721A. The last segment of the tail and the sting were sawn off the nodule and developed separately. They were mounted in Marco on glass as 721C.

The half labelled B originally exhibited bits of dorsal skin, the natural cast of the inside of the dorsal skin, and indications in places of ventral organs, all seen in dorsal view (Pl. 50, fig. 1). After development it displayed many ventral organs in ventral view together with traces of the dorsal features as impressions in the Marco-cast (Pl. 50, fig. 2; Pl. 51, fig. 4). The Marco-cast has now been filled in as a Marco-block, B.U.721B.

The specimen was remarkable for its large size—about 7 cm. in length—and is so now for the complete preservation of almost every part, like an insect in amber, within the three Marco-blocks. The missing organs, except for parts of the ventral skin which is probably present but crushed on to the dorsal tergites, can be accounted for as follows. Part of one sternite fell away, but was recovered; and I extracted and mounted the left halves of two sternites in order to be able to examine them in transmitted light. I also recovered the end of one leg, fragments of the finger of one pedipalp, and a few tiny bits of other parts.

Diagnosis of genus and species. Large Orthostern 'scorpion', *c.* 70 mm. long and 11 mm. wide at widest tergite XI; dorsal side and prosomatic appendages conforming to the pattern of a Recent buthid scorpion with a long sting, large chelicerae, powerful pedipalps, and slender legs which have the buthid arrangement of spurs.

Carapace almost square with a median groove and two cephalic and two postcephalic arched lobes; median eyes small on front of an eye tubercle of two kidney-shaped bosses separated by a narrow groove, close to front margin of carapace; front part of carapace has deep doublure and is coated with fine hairs, rear part covered irregularly with small granules which are tiny on the postcephalic lobes. Tergites coated with fine hairs, otherwise unornamented. Tergal plate XIII and all caudal rings with strong dorsal keels, caudal ring XVIII short, sting long, flask-shaped with strongly curved aculeus.

Chelicerae large, projecting in front of the carapace for a distance equal to not less than half its length. Pedipalps powerful. Coxo-sternal area with a bluntly pentagonal sternum; mandibular process of 1st leg larger than that of 2nd, coxa 4 about twice the length of coxa 3; legs relatively slender, coated with fine hairs, two denticulate claws and two tarsal spurs on each leg; one metatarsal spur on 3rd and 4th legs.

Genital operculum with two pairs of arched lobes and a narrow median ridge carrying a flattish leaf-shaped plate. Sternum of pecten ill-defined, combs large, each with at least sixteen teeth. Sternites roughly rectangular, overlapping backwards. Sternite IX ill-defined, possibly triangular behind. Sternite X lamellate, in two halves, each half with deep posterior doublure, rounded at postero-lateral corner and here covered externally and on doublure by minute hairs; no stigmata. Sternites XI, XII similar to Sx, but possibly not divided into two halves. Sternal plate XIII large with pronounced rounded postero-lateral corners, possibly half the plate was covered by Sxii.

Description. The carapace measures 8 mm. in length and 9 mm. in breadth behind. The abdomen is 20 mm. long and 10 mm. wide at its widest part (tergite XI). The tail, as preserved in A, is *c.* 20 mm. in length, but a few mm. were lost in the sawcut that severed the last caudal ring and tail. The last caudal is 5 mm., and the sting can be estimated at not less than 15 mm. These figures give the total length of the 'scorpion' as 68–70 mm.

Dorsal surface

Prosoma. Carapace (Pl. 49, fig. 3; text-fig. 10). This is nearly rectangular, with a slight taper forwards. The front corners are rounded and devoid of lateral eyes. The anterior

margin has a slight median projection. The whole front end has a very deep doublure extending back at least as far as the hind end of the eye-tubercle. The carapace was originally rather strongly arched with a deep median and two slight postcephalic grooves, which together divide the shield into two lobes of the cephalic region in front, and a pair of postero-lateral postcephalic lobes behind. The median groove narrows in front where it is continued as a narrow furrow between the two halves of a small circular eye-tubercle, situated very near to the front margin of the carapace which it overhangs. The small eyes, originally hemispherical and looking upwards, occupy the front half of the tubercle. The posterior margin of the carapace is a broad band of thick skin rounded at the corners, with a few small hair-bases. Many parts of the skin of the shield are ornamented by numerous small granules which show up most prominently on the folds at the sides of the grooves. The postcephalic lobes, however, are covered with similar, but quite tiny granules. Numerous hair-bases, some with short setae still attached, occur on the external surface of the R. anterior corner (some also are probably on the doublure). In addition, the original existence of a coating of minute fine hairs over much of the front end is evidenced, where the chitin of the shield is missing, by the actual hairs (now attached to the Marco-cast) which were torn from their bases but left in the rock when the skin was broken away. A similar coating of fine hairs has been observed in other parts of the animal (below).

EXPLANATION OF PLATE 49

Figs. 1–7. *Mazoniscorpio mazonensis* gen. et sp. nov., B.U.721A. 1, Ventral view of dorsal skin, as received. Photographed under alcohol. ×2·7. 2, Dorsal view of dorsal skin and R. appendages after development. ×2·7. 3, Chelicerae, carapace, and tergite VII, after development (cf. text-fig. 10). ×5. 4–7, The ends of the four L. legs, fig. 4 being the 1st and fig. 7 the 4th, photographed during development. ×7.

For key to abbreviations see p. 277.

EXPLANATION OF PLATE 50

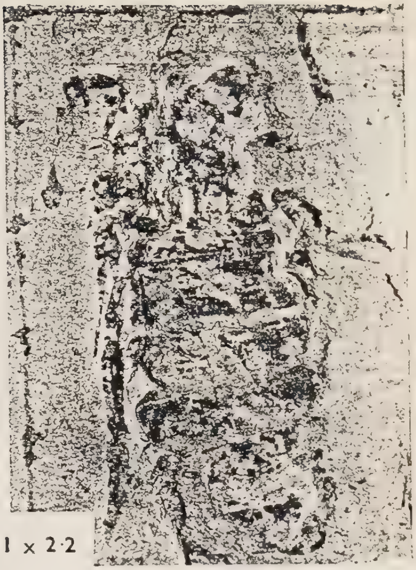
Figs. 1–5. *Mazoniscorpio mazonensis* gen. et sp. nov., B.U.721B except figs. 3, 4 (fragments derived from 721/A). 1, Dorsal view of dorsal skin and in places traces of ventral features. As received, ×2·2. 2, Ventral view of the ventral organs of anterior part of the body before detachment of sternites, and of the Marco-cast containing bits of chitin and impressions of dorsal and ? ventral skin of the posterior end (cf. text-fig. 12). ×5. 3, Tip of the fixed finger of the hand of the R. pedipalp. Slide B.U.721A/4/6. ×40. 4, Metatarsus with spines and tarsal spurs, tarsus and claws of 2nd or 3rd leg, showing hairs and hair-bases. Slide B.U.721A/3. ×14. 5, Fragments ? left side of sternite ? XII, figured on Pl. 6, fig. 6; photographed by transmitted light to show hairs on both surfaces. Slide B.U.721B/1. ×40.

For key to abbreviations see p. 277.

EXPLANATION OF PLATE 51

Figs. 1–3. *Buthiscorpius major* sp. nov. G.S.M. Za 2926. 1, As received. Ventral view of dorsal surface, photographed under alcohol. ×3. 2, 2nd Marco-cast often etching. Dorsal view of dorsal surface of body, with tergites VII–XII and two fragments of the sting. ×3. 3, 1st Marco-cast repaired, dorsal view of dorsal surface of body and tail, after etching. ×3.

Figs. 4–6. *Mazoniscorpio mazonensis* gen. et sp. nov. 4, B.U.721B. Progress photo of ventral organs to show the L. pedipalp and L. legs with claws and spurs. Some parts outlined in ink. ×2·1. 5, Ventral view of the skin of the L. ends of sternites ? X, XI, with the posterior margin and median continuation of ? SX. Slide B.U.721/2. ×6·8. 6, Part of the L. side of ? SXII having hairs on both sides (see Pl. 50, fig. 5). Slide B.U.721B/1. ×6·8.



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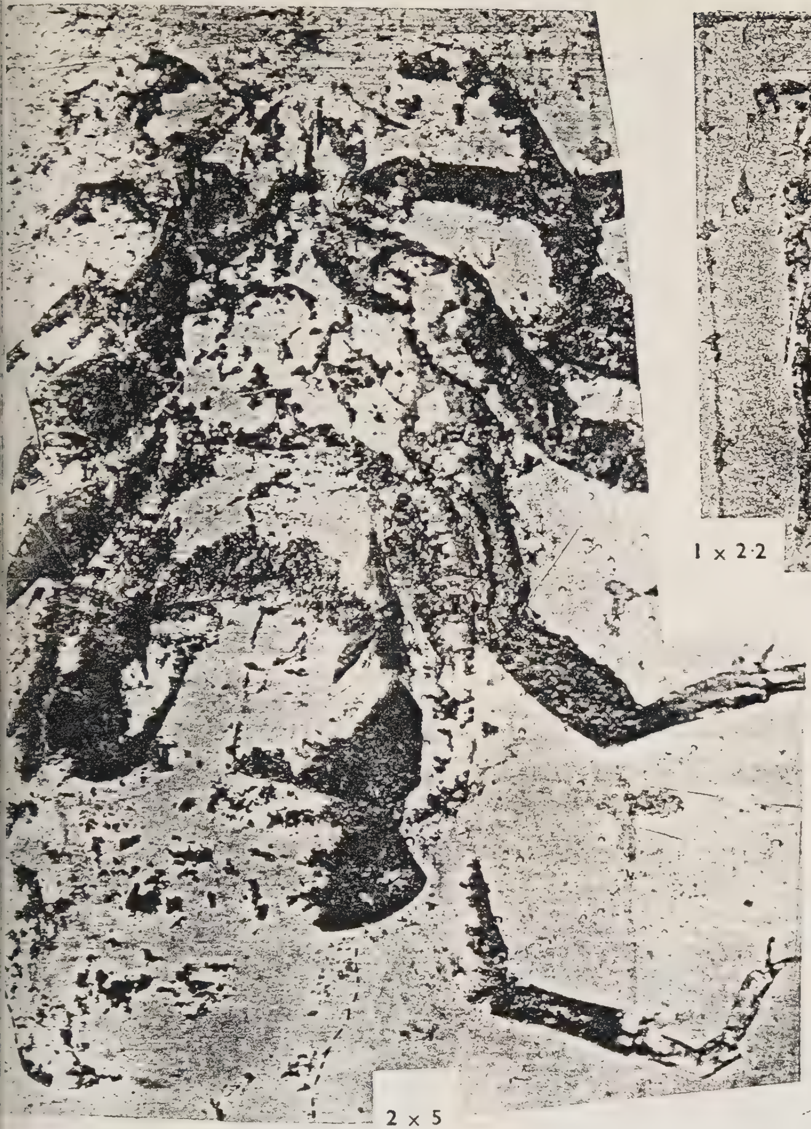

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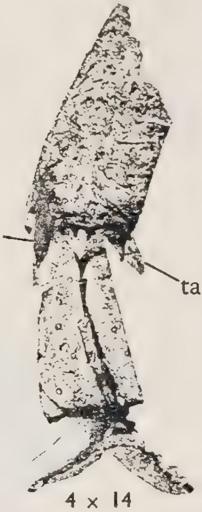

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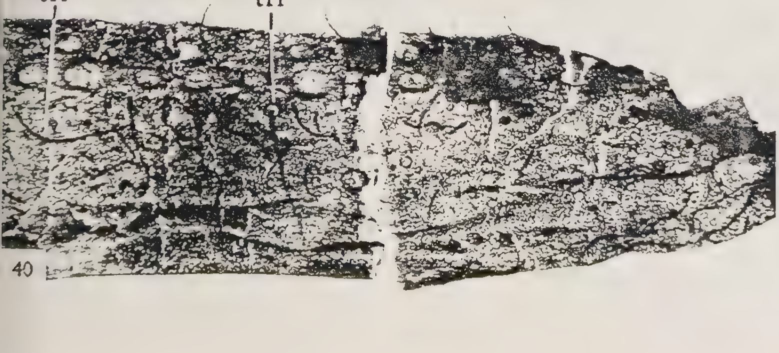

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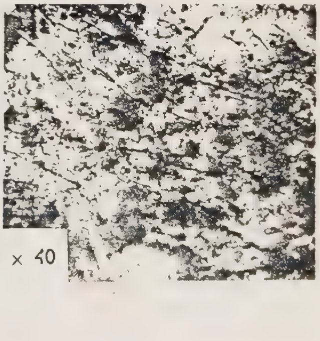

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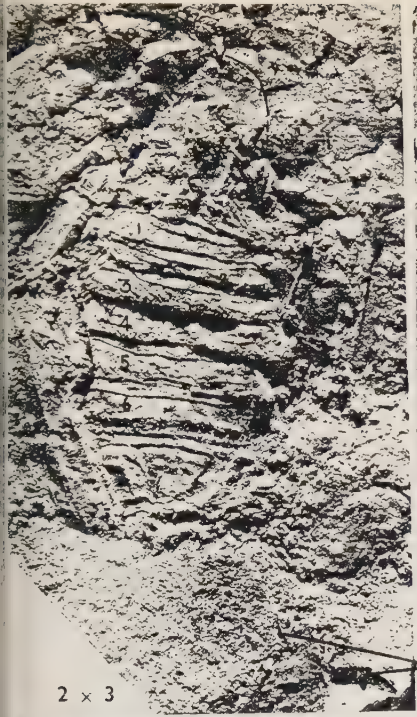

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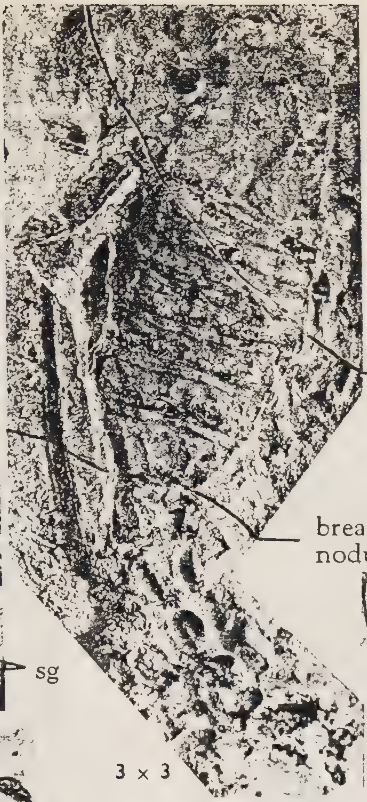

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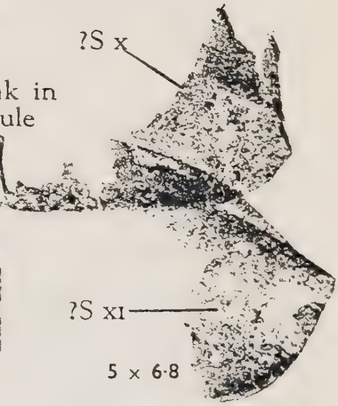

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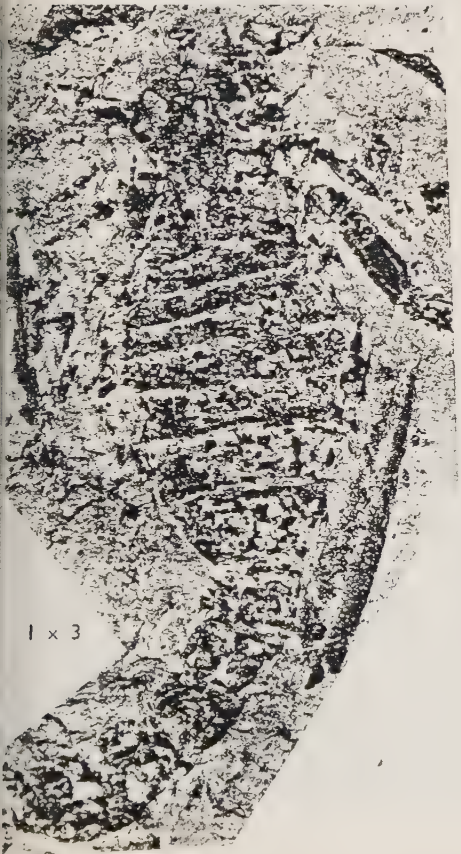

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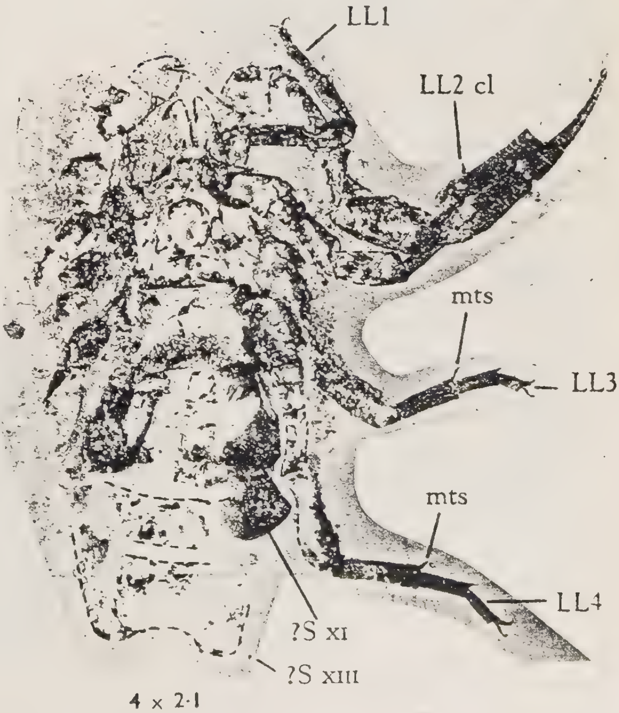

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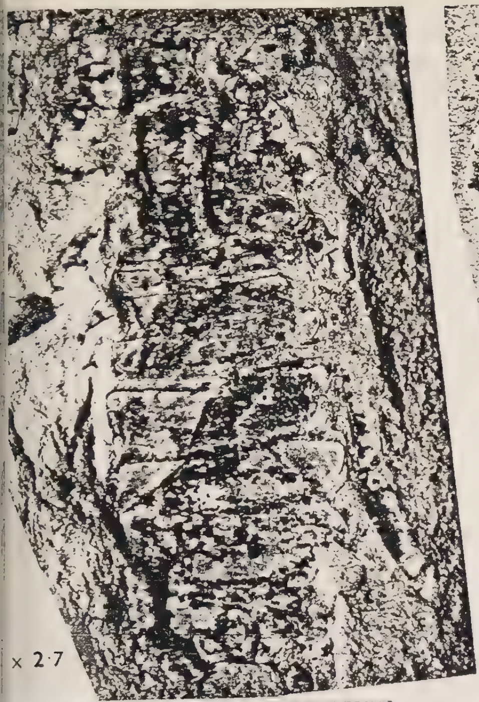
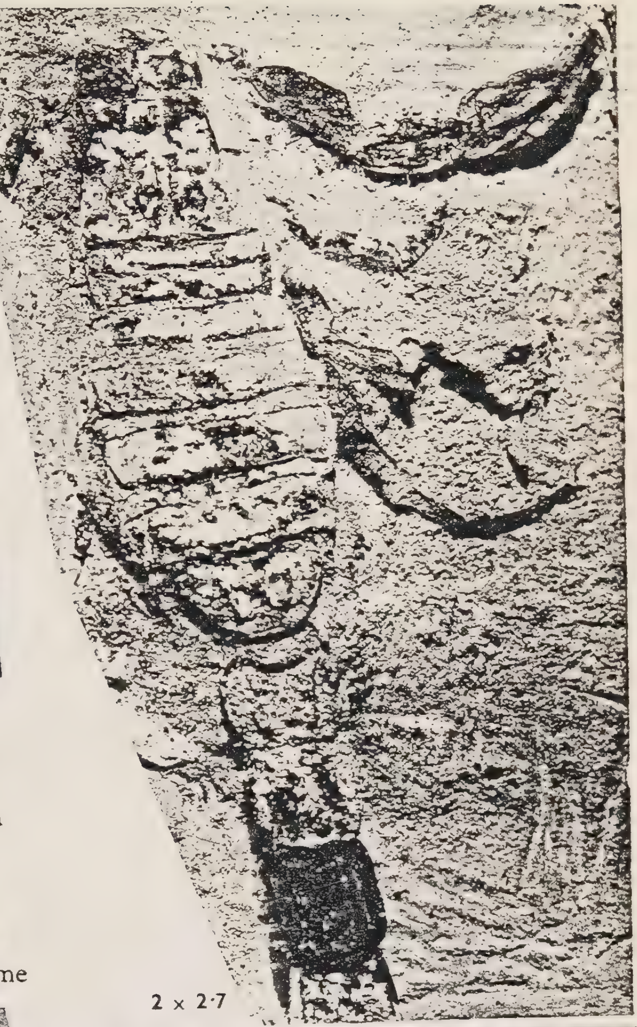


× 2·7



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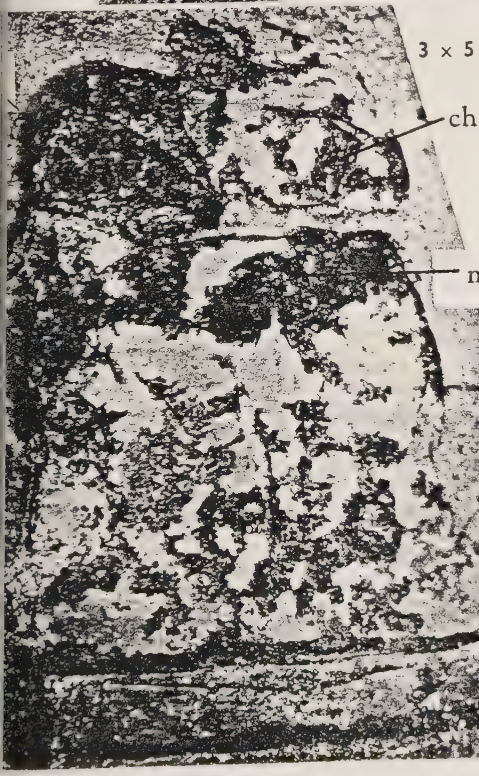

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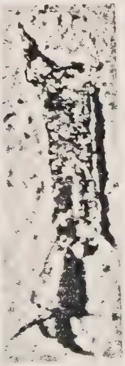
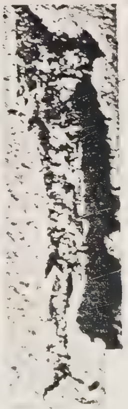


4 × 7



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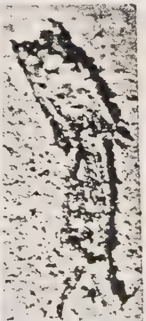
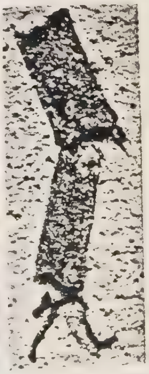


6 × 7



7 × 7

Mesosoma. Tergites VII–XII (Pl. 49, figs. 1, 2). These are quite normal in shape and roportions, increasing in length backwards from 1 mm. to 3 mm., and in breadth from e carapace to tergite XI and then decreasing slightly. Each is bounded by a linear nterior margin and an unornamented posterior margin formed by a narrow infold or oublure which passes into the wide anterior border of the next segment. These margins ginally appeared as rather wide lines (Pl. 49, fig. 1). They carry, possibly on the ublure, a few small hair-bases. The surface of the tergites is devoid of granules, but e a uniform coating of minute hairs without visible hair-bases, which is similar to t on the front of the carapace. There are folds across the ends of some of the tergites ich suggest that in life they were strongly arched from side to side.

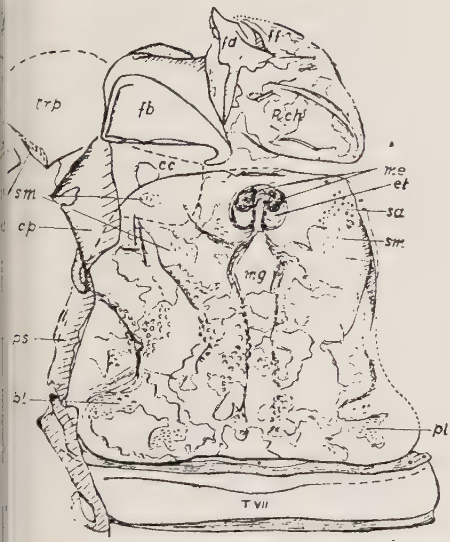


FIG. 10

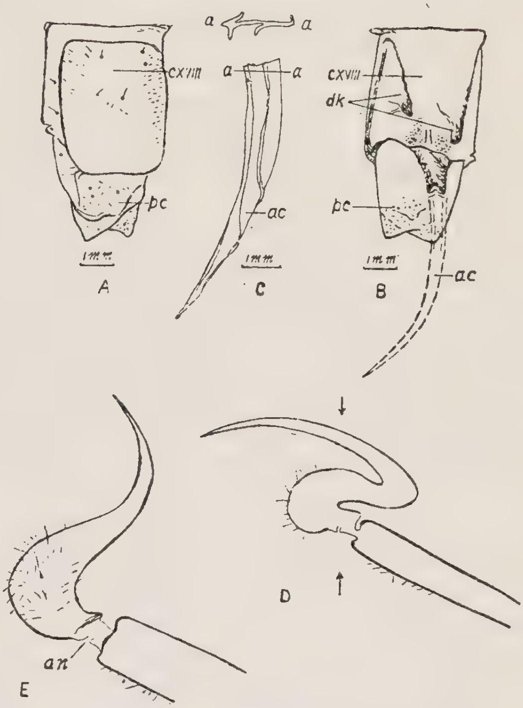


FIG. 11

T-FIG. 10. *Mazoniscorpio mazonensis,* gen. et sp. nov. B.U.721A. Chelicerae, carapace, and 1st gite. × 5. *cc,* coxa of L. chelicera outlined by broken line; *cp,* coxa of L. pedipalp; *et,* eye-tubercle; finger of L. chelicera bent backwards; *fd,* fixed finger of R. chelicera; *ff,* free finger, ditto; *fp,* femur L. pedipalp; *me,* median eye; *mg,* median groove; *pl,* posterior lobe covered with minute granules; pleural skin; *R.ch,* right chelicera; *sa,* setae and hair-bases of ant. outer skin; *sm,* short setae of *sa* in Marco; TVII, tergite of 7th segment.

T-FIG. 11. *Mazoniscorpio mazonensis* gen. et sp. nov. B.U.721C. Pre-anal caudal ring (CXVIII) and son-capsule (*pc*) and aculeus (*ac*) of the sting. A, In ventral view showing the shield-like surface of VIII and the folded ventral surface of the capsule. B, Dorsal aspect with aculeus (broken line) ored to its original position, *dk,* dorsal keel. C, Aculeus in plan and section. D, Sagittal diagram-ion of present postures with spaces between the crushed skin opened up. Arrows show direction of crushing pressure. E, Tentative restoration, anus (*an*).

Metasoma. Tergal plate XIII. The outer surface of this was completely exposed by the

etch. It has the normal outline, rapidly narrowing backwards to about one-third its anterior breadth to accommodate the 1st caudal ring. It carries a pair of strong, knobbly dorsal keels which end well in front of the true posterior margin at points where they meet a transverse ridge that mimics the appearance of the real margin. As a result of having these keels, the tergal plate resembles the dorsal sides of the caudal rings. Assuming that the keels were for muscle attachments, it would appear that the arching of the tail and sting over the body of the 'scorpion' involved the last segment of the abdomen as well as the caudal segments.

Metasoma. Sternal plate of segment XIII is poorly exposed, most of its chitin having been lost or else pressed against the inside of the tergal plate. From what is left in specimen B it appears to have been wider than the latter and to have ended in two postero-lateral processes (Pl. 51, fig. 4).

Caudal rings and sting (Pl. 49, fig. 2; text-fig. 11). Caudal rings XIV-XVII etched out complete as a sort of bridge from the body to the wall of Marco to which CXVII was attached (i.e. the sawcut referred to above). It was not feasible to clear all the matrix from below the bridge, and for that reason they can only here and there be viewed by transmitted light, and details of their ventral sides are unknown. Owing to compression the rings appear wider than they originally were. Each carries a pair of strong dorsal keels (it cannot be seen that these are denticulate) and a pair of lateral or dorso-lateral keels. They all resemble closely the corresponding rings in *Buthiscorpius buthiformis* (text-fig. 2).

The caudal ring of the pre-anal segment XVIII and the sting are preserved in specimen C (text-fig. 11). The caudal ring is short and this may be due to the sawcut that severed it from specimen A, but it appears to be complete. It is not much longer than the preceding ring, and in this respect differs from the corresponding segment in *Buthiscorpius*. As the ring and sting are completely transparent every detail can be examined. The dorsal surface of the ring has two short, posteriorly elevated dorsal keels, but is otherwise devoid of conspicuous features, except for a dark blotching of the skin and two minute longitudinal folds at the distal end (text-fig. 11B). These may have led to a median sinus on the posterior margin, but this, if present, is concealed by the folded sting. The blotching and folds recall features seen in the pre-anal segments in *Mesophonus* (Wills 1947, p. 69, text-fig. 34). The ventral surface in its flattened state is clearly seen to have an almost rectangular shield-like shape that is defined by folds at the front and sides, and by a strong posterior margin and doublure behind. Near this margin were long setae, a few of which are still in place. In addition there are on various parts of the ring several small sensory hairs (one still in place) attached to hair-bases, and many short hairs like those that coat the front of the carapace and the tergites. These latter appear to be on the ventral surface only.

The sting (text-fig. 11) consists of a crushed and crumpled, originally flask-shaped, poison-capsule and a long, strongly curved aculeus. The latter is now broken away from the neck of the capsule, but was seen during development to rise vertically from it (the neck is still visible in this position, but the broken aculeus had to be mounted on its side). As found, the aculeus pointed distally with its concave side ventral. To attain this posture (text-fig. 11D) it must have been inverted during the consolidation of the rock by pressure applied to the whole sting as it stood up almost vertically over the pre-anal ring in the posture usually to be seen in dead scorpions. In the capsule various folds of

skin can be seen, but its exact original shape is hard to determine. Text-fig. 11E ws a possible reconstruction. Some parts of it are closely covered by numerous small r-bases, often with short setae attached. The aculeus itself (text-fig. 11C) tapers dually to a fine point. Its smooth, thick chitin is folded longitudinally in a way that ngly suggests that it contained a pair of poison-ducts (as is the case in Recent scor- ns and in the Triassic *Mesophonus*. See Wills 1947, p. 75.) Near the base of the ken part of the aculeus is a single tiny hair-base.

tral organs

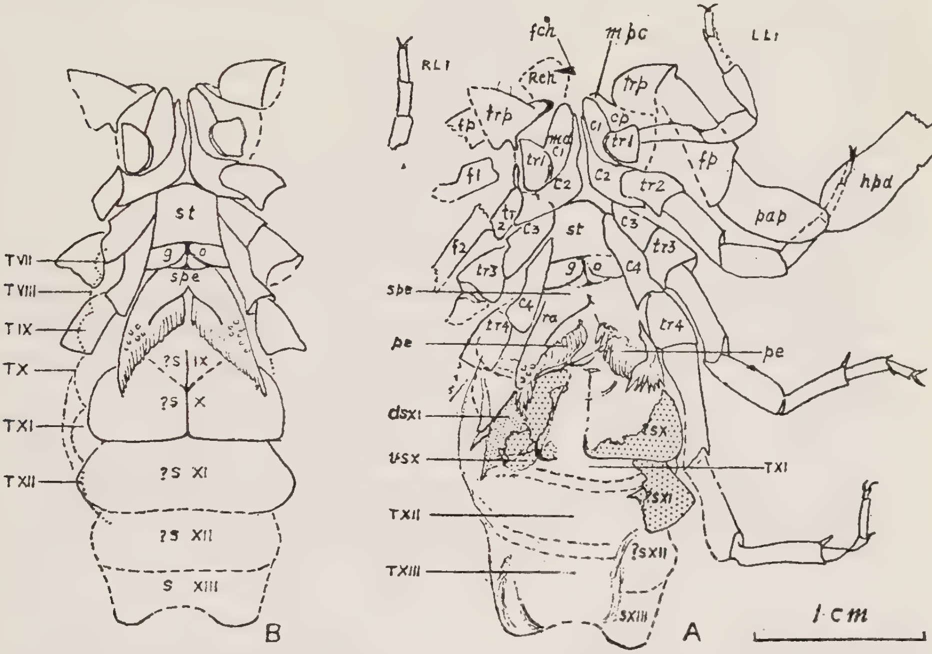
s appears to have been the case in several of the 'scorpions' developed, the original ture of the nodule followed the inside of the dorsal skin, and where the ventral n had been closely apposed it suffered some damage. In the present case most of the tral organs can be seen in specimen B as far back as the last sternite (SXII), but im- tant parts of them are damaged or missing, so that some uncertainty as to their pes is inevitable.

he ventral half as originally exposed in dorsal aspect is shown on Pl. 50, fig. 1. The lines of parts of the chelicera, of the two pedipalpal trochanters, of the mandibular cesses of coxae 1 and 2, the end of the 1st R. leg, and bits of other appendages could made out, but after development many other features appeared (Pl. 50, fig. 2; Pl. 51, 4; text-fig. 12), most of which are still visible in the Marco-block B.

rosoma. Chelicerae. These show best in specimen A (Pl. 49, fig. 3; text-fig. 10). The al joint of the L. chelicera can be seen to lie below the left front corner of the cara- e, followed by the hand which appears to have been bent backwards on itself (text- 10). The hand of the R. chelicera shows the distal parts of the fingers, while their can be seen in specimen B (it is possible that the tips referred to belong to the L. icera). The hands are at least half as long as the carapace (cf. *Lichnophthalmus* in t 1, p. 288). In specimen B the Marco-block carries many short hairs scattered over impression of the R. hand, and one or two larger ones on the fingertips.

edipalp. The original fracture damaged the coxae and trochanters of the pedipalps, their general shape can be seen to be quite normal. The distal ends of the coxae ied rather large hairs (? trichobothria) and so did the trochanters which also have a ting of smaller bristles like those on the carapace, tergites, &c. The rest of the endage consists of massive articles of the normal shape in Recent scorpions. The le R. hand except the very tips of the fingers is preserved in specimen A, and in B the ne is complete save for the end of the fixed finger, but bits of the missing part were vered (Slides A/4, A/6; Pl. 50, fig. 3). The mounts show that there was a row of large ules along the biting edge with a second row of widely spaced still larger ones her from the edge, a few long, slender, certainly trichobothrial bristles and numerous ller ones without conspicuous bases, and that the skin was thick and markedly ular in texture. The femur, patella, and palm of the hand have few or no hairs that be seen. The patella and hand are crumpled by several large lengthwise folds which ly that in life both were strongly keeled. No 'stop-knob' can be seen on the patella. hese features can be matched in large Recent forms, in *Buthiscorpius major* (Pl. 52, 3), and in *Lichnophthalmus* (Part 1, p. 278, pl. 49, fig. 7). The general shape is also h the same as in *B. buthiformis* (Pl. 47, fig. 3) which, however, is relatively shorter , perhaps because of its small size, has no granules on the biting edges.

The coxo-sternal region and legs. These only differ in minor points from those of certain Recent Buthids and from the other Carboniferous Orthosternid 'scorpions' here described which show these organs, in particular *B. buthiformis*, B.U.720. The relation of coxae to the sternum is that stated by Petrunkevitch (1955, p. P73) to characterize the superfamily Scorpionoidea Leach 1815, namely—'First and 2nd pairs of coxae with well-developed maxillary lobes (fig. 40, 1), those of the 2nd pair meeting in median line and wedged in between maxillary lobes of 1st pair; 3rd and 4th pairs of coxae abutting against sternum'. His fig. 40, 1 is based on one of Pocock's paratypes of *Buthiscorpius buthiformis* (B.M. In. 1555).



TEXT-FIG. 12. *Mazoniscorpio mazonensis* gen. et sp. nov. BU.721B. A, Ventral view of the ventral organs with the positions of some dorsal elements (broken line), cf. Pl. 50, fig. 2, Pl. 51, fig. 4. B, Tentative restoration of the same, the existence of the plate marked ? Sxii being in doubt. *d*Sxi, internal (dorsal) skin of the pouch above Sx (this skin belonging to Sxi); *fch*, finger of ? R. chelicera; *mpc*, maxillary lobe of coxa of pedipalp; *v*Sx, internal (ventral) skin of the pouch above Sx pressed against the external skin of the same. For key to other abbreviations see p. 277.

The coxo-sternal region and the left legs are well seen in specimen B (Pl. 50, fig. 2; Pl. 51, fig. 4; text-fig. 12).

The *sternum* is pentagonal with its two anterior edges, defined by the back edges of the two coxae 4, making an angle of 130°, and with its posterior edge slightly emarginate where it adjoins the genital operculum. Against its sides abut coxae 3 and 4.

The big coxae of the *pedipalp* appear, in ventral view, to underlie the mandibular processes of coxae 1 and 2. The maxillary process of the L. pedipalp with a few largish hair-bases is well exposed (text-fig. 12, *mpc*). The mandibular processes of the *1st leg* are much broader than those of the *2nd leg* (in Recent scorpions the reverse is the case). Both processes have a felt of minute hairs on the inner sides of their tips. The rest of

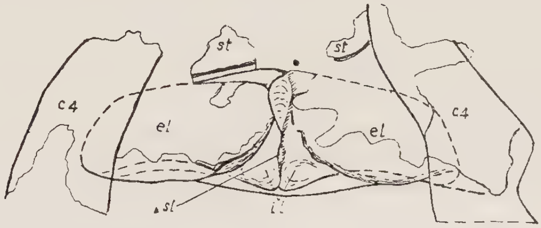
a 1 is small, little more than an articulation for the small trochanter. In contrast the ıll mandibular processes of coxae 2 pass into large horn-shaped articular ends, the terior sides of which define the front of the sternum. The coxae of the 3rd and 4th abut against the sides of the sternum, that of the 4th leg being about twice as long hat of the 3rd. The two on the L. side seem to be still united, whereas there appears e a gap between those on the Right. This appearance is probably the result of the or fracture of the thin connecting chitin.

he four L. legs are preserved virtually complete in specimen B (Pl. 51, fig. 4), but in cimen A all the R. legs except the 3rd are broken (Pl. 49, fig. 2). In general shape proportions all are closely similar to the much smaller ones described in *B. buthinis*, but nearly every joint can be seen to be covered with a felt of small setae comable with those on the carapace, tergites, &c., and the claws are denticulate, as in all larger specimens here described. The pads (*Gehstachel*) at the base of the claws are e small, as in other orthosterni. Spines, sensory hairs, and spurs on the intersegıtal skin at the base of the tarsus and metatarsus are conspicuous and arranged as in *uthiformis* (p. 289), in particular two tarsal spurs on all four legs, and a single metaal spur on the 3rd and 4th. The ends of the four legs were displayed simultaneously ne stage of the etching and were photographed (Pl. 49, figs. 4–7). The figures show the tarsus gets progressively longer with the increase of length of leg from the 1st th. That on the second appears to be very slender, but this may be due to an accident reservation. Details of the claws, spurs, spines, and sensory hairs (? small trichohria) are well shown on the end of the 2nd or 3rd R. leg which broke loose during the ing of specimen A. Mounted as Slide A/3 (Pl. 50, fig. 4) it displays very clearly the y ends of the sides and lower surface of the metatarsus, a feature not noticeable in metatarsus of other specimens, but one that I note below as being conspicuously eloped on the tibia of the 3rd leg of G.S.M., Za 2924 (text-fig. 19E). Slide A/3 also es clear how the pad is connected by prominent ridges to the bases of the claws.

osoma. There is very little ventral skin preserved behind the genital operculum and not easy to trace any margins to the sternum of the pecten and the first sternite). The next two were better preserved, their L. postero-lateral parts having etched out . I photographed them under water (Pl. 50, fig. 2, Pl. 51, fig. 4) to obtain a record. n in order to be able to examine them from both sides, and because they appeared e almost detached by the solution of an underlying (in ventral view) film of matrix, ised them away without breaking them and mounted them as Slide B/2 (Pl. 51, fig. 5). he point on the Marco-cast from which the supposed Sx was detached, there is an covered with thin chitin. Somewhat similar, but less distinct patches follow where next sternite (Sxi) was lying and where the supposed last sternite (Sxii) is indicated ext-fig. 12. I think that the fragment of sternite mounted as Slide B/1 (Pl. 51, fig. 6) be the L. end of Sxii, derived from above this last patch, but its exact provenance is nown. If I am right in this interpretation, Sxii would in ventral view lie partly over and partly over Txiii, as shown in text-fig. 12. If I am wrong, those segments ked ?S ix–Sxi must be in reality Sx–Sxii, and the part marked ?Sxii must be merely front half of Sxiii.

ccepting my preferred interpretation (text-fig. 12) the following features may be ed.

The *genital operculum* (text-fig. 13) is a complex organ, the skin of which is still preserved in slight relief. It is almost oval in outline with the anterior edge making an obtuse, forward-pointing angle. This edge at one point can be seen to be parallel to the posterior margin of the sternum. Both its sides are obscured by the flattened 4th coxae. The posterior edge curves gently backwards near the middle line, is overhung by the external lobes (see below), and is inturned as a narrow doublure. The whole operculum is clearly a bilaterally symmetrical organ consisting of two pairs of lobes, the two external ones (*el*) being arched and falling away towards the posterior margin and towards the two internal lobes (*il*) which are also slightly arched. Down the middle line is a continuous narrow ridge or keel which, towards the front, carries a leaf-shaped flattish structure. Behind this the ridge at one point shows a narrow slit which may represent the opening of the genital duct, but is more probably an accident of fracture.



TEXT-FIG. 13. *Mazoniscorpio mazonensis* gen. et sp. nov. B.U.721B. Parts of the sternum, genital operculum, and the two coxae 4. ×10. *c*4, coxa 4; *el*, external lobe; *il*, internal lobe; *sl*, slit in median ridge; *st*, sternum.

With this specimen before us it is now clear that the structure in *Lichnophthalmus pulcher* Petr., tentatively interpreted as an anterior plate of the sternum of the pecten (Part 1, p. 272, text-fig. 4), is really the genital operculum, since it also consists of two pairs of lobes with a median ridge. I pointed out the possibility that this might be the case, and noted that, should it turn out to be so, then coxa 4 lay alongside the genital operculum (as is the case here), and did not abut against it as it does in *Pareobuthus*, *Eobuthus*, and other 'Isobuthidae'. See also Addenda, p. 331.

Behind the genital operculum, on the 8th adult segment, the *sternum of the pecten* is poorly defined, but appears to have been short. It carried a pair of large combs on which the raches are very broad at their bases but taper to a point. Possibly both combs have been broken and the teeth displaced backwards near the middle line. The rachis carried, at any rate distally, bosses with sensory hairs (a feature common to all the combs examined); fulcra cannot be recognized but may well exist; sixteen teeth canbe counted on the L. comb.

Behind the sternum of the pecten a long stretch of the ventral skin, partly destroyed and partly covered by the combs, could easily account for two sternites, but I think it was more probably occupied by a single large one (the supposed *sternite* IX), the posterior margin of which was a broad V evidenced by a groove in the Marco. Since the median suture of Sx can be traced across it, the groove may indicate the limit of the area on Sx covered by the V-shaped end of S IX.

Much of the supposed sternite X has survived. It was a roughly rectangular flat lamellate organ with a median division (perhaps in the form of a suture) and a small

ian posterior notch between the two halves. (It is interesting to note that in *Pareo- us* sternite x also shows a line of very thin skin between its two lobes, which ars to be absent from the other sternites. Wills 1925, pl. 3, fig. 2.) Much of the L. was originally seen in place (Pl. 50, fig. 2; Pl. 51, fig. 4), but is now mounted as Slide Pl. 51, fig. 5). The R. half had been displaced and crushed sideways, but many of etails can still be seen in the Marco-block (text-fig. 12A), including indications of nedian notch.

nly the R. end of the supposed sternite xi was seen during the etching, and this came y attached to the adjacent piece of sternite x (Slide B/2, Pl. 51, fig. 5). As noted e, another end of a sternite was detached by the etching before its position had been ed. It may be the L. end of sternite xii, but it could equally well be the R. end of nite xi. Here it is regarded as the L. end of sternite xii (Slide B/1, Pl. 50, fig. 5; Pl. 51,). Sternites xi, xii are very badly preserved, and no sign of a median suture can be . The absence of chitin is due to the ventral skin having been pressed against the al, and the two having broken away from specimen B. The ventral skin can be seen aces in specimen A, but no details can be made out.

text-fig. 12A I have shown by broken lines the position of the intersegmental skin een tergites xi, xii, and the tergal plate of segment xiii, and on text-fig. 12B the ends ll the tergites, as in specimen A. From these it will be seen that on the proposed pretation each sternite covers not only its corresponding tergite, but about half of ext one behind, Sxii eventually concealing the front half of Sxiii, which last is only esented by a few scraps of chitin, whereas the whole of tergal plate xiii is preserved ecimen A (Pl. 49, fig. 2). Each overlap formed a pouch opening to the sides and nd. Some parts of the overlapping portions of each of the supposed sternites x–xii be examined—the L. ends as Slides B/1 and B/2 and the R. end of Sx in the Marco- k B. In every case they consist of an external layer and a large thin-skinned doublure, in B/1 and B/2 both surfaces can be seen to be covered closely by a felt of very ite hairs (Pl. 51, fig. 6). At the L. end of Sx, a patch of thin chitin can be seen in Marco-block at the point from which Slide B/2 was detached, and a similar patch vs at the right end where sternite x has been displaced (text-fig. 12A, *d*Sxi). These egarded as the dorsal or inner linings of the pouches, the skin itself being the over- ed portion of the next segment behind. On the same figure the letters *v*Sx point to rumpled and displaced outer skin and doublure of the overlapping Sx.

hese observations appear to prove that at either end of each sternite the postero- al corner concealed a pouch, the ventral lining of which was the posterior doublure at sternite, and the dorsal lining of which was the anterior part of the next sternite nd (or the sternal plate, Sxiii, in the case of the last one). In this respect the sternites pare exactly with the leaf-appendages (*Blattfüsse*) of *Eurypterus*, but the overlap g relatively narrower they had less freedom of movement, and were correspondingly e like true sternites than leaf-appendages. The general arrangement also matches ely the structure of the sternites in *Pareobuthus* (Wills 1925) and *Lichnophthalmus* t 1, p. 274), though the sternites in the present case are not bilobate, and have hairs ead of spinelets on the doublure.

nagine a gill within each pouch and we have a structure comparable with that of a *tfuss* of *Eurypterus fischeri* Eichw. as described by Holm 1898. The available space he gill, however, would seem to be relatively much smaller than in *Eurypterus*, and

the sternites ill-adapted to promote a circulation of water through the gills. Such an interpretation would nevertheless seem to imply a truly aquatic life for this particular Orthostern 'scorpion', an environment similar to that inferred for the Lobosterni described in Part 1.

Alternatively, imagine some air-breathing organ, perhaps a lamellate structure akin to a gill-book, occupying the pouches and protected from drying up by the close-fitting, hair-covered corners of the 'sternite', and we have an arrangement that can be pictured as a first stage in the evolution of a scorpion's lung-books. By the fusion of the outer edge of the first sternite to the overlying 'sternite', except for a short strip at either end, the arrangement found in the Triassic *Mesophonus* could follow. Here the lung-book opening (stigma) is either on the postero-lateral margin or on the adjacent doublure that connected that sternite to the next one behind (Wills 1947). Starting again from that arrangement, it is easy to postulate a simple migration of the stigma from the edge to the outer surface of the sternite to account for the siting of the pulmonary opening in present-day scorpions.

On this second hypothesis this particular Orthostern 'scorpion' would rank as an air-breather, though probably only adapted to life in a moist environment.

There is no satisfactory evidence as to which hypothesis is correct, but the amount of overlap in the present case is greater than in *B. buthiformis*, and large enough to make me favour the aquatic one.

SECTION B—ONLY HALF-NODULES AVAILABLE

Buthiscorpius major sp. nov.

Plate 51, figs. 1–3, Plate 52; text-figs. 14–16

Holotype. G.S.M. Za 2926. Coal Measures (Ammanian), base of *Communis* Zone, Kilburn Coal, Trowell Colliery, Nottinghamshire.

Remarks. As originally exposed, there were visible most of the carapace, the mesosomatic tergites, the tergal plate of the 13th segment, all the caudal segments of the metasoma except the sting, and several bits of the legs (Pl. 51, fig. 1). After photography the specimen was embedded in Marco, but during the grinding away of some unwanted matrix, the Marco-mount cracked right across, and a fresh start had to be made. In trying to extract the nodule from the cracked mount the specimen was broken in two, but *not at the place* where the mount had split (Pl. 51, fig. 3). The rock containing the tail adhered to the Marco, and was later developed by solution. This first mount with its cracks repaired provides a record, in the form of a cast, of what was originally visible and also of what was etched-out in the caudal region. It is referred to in the sequel as the *1st Marco-cast*.

The part of the nodule which broke away from this first mount contained the body and appendages. It was remounted and developed by solution, and after several parts of the scorpion had been extracted, the second mount remained as the *2nd Marco-cast*. Parts of the sting and of one leg, however, were

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EXPLANATION OF PLATE 52

Figs. 1–5. *Buthiscorpius major* sp. nov., G.S.M. Za 2926. 1, L. chelicera and pedipalp minus its coxa, in dorsal view. Slide Za 2926/1. ×10. 2, R. pedipalp minus its coxa in dorsal view, except the broken end of free finger which was inverted in mounting. Slide Za 2926/2. ×10. 3, Tip of the free finger of L. pedipalp in ventral view. Slide Za 2926/1. × 66. 4, Hand of the L. chelicera in ventral view. Slide Za 2926/1. ×66. 5, Coxa (below) and trochanter of ?3rd or 4th R. leg. Slide Za 2926/3. ×10.

For key to abbreviations see p. 277.

attached to it in their original positions and can still be seen in place (Pl. 51, fig. 2). It was surprising
ind the sting on this Marco-cast as the rest of the tail was etched out on the 1st Marco-cast. It must
e been bent back over the tail since the aculeus points towards the head of the scorpion.

t first it was assumed that the visible dorsal organs were exposed in dorsal aspect on the half-
lule, but on development it was found that in fact they were exposed in ventral view, for the 2nd
rco-cast has the eye tubercle projecting upwards and the tergites overlapping one another back-
ds as ridges (see text-fig. 14 and Pl. 51, fig. 2). This explained the disappointing fact that the ventral
ts—the sternum, genital operculum, pecten, and sternites—were not discovered during develop-
nt. They lay in the other half-nodule which had not been collected. However, one chelicera, both
ipalps, and the coxa and trochanter of the 3rd or 4th right leg were isolated with the original
wn chitin virtually free from matrix. Their most intimate details of structure can be examined in
nsmitted light (Pl. 52), and it can be demonstrated that these parts were organized in Carboniferous
es on almost exactly the same lines as they are in a Recent buthid scorpion.

. major is undoubtedly an Eoscorpioniid comparable with *Eoscorpius* Meek and Worthen, *Buthi-*
rpius Petr., and *Compsoscorpius* Petr. The carapace of the holotype of *E. carbonarius* lacks its front
, and so comparison with it in respect of the shape and proportions of the carapace, and the posi-
n and nature of the eyes is precluded. I thought at one time the present specimen showed one or
re lateral eyes, but am now convinced that I was mistaken. Had lateral eyes been present the speci-
n could be ascribed with assurance to *Compsoscorpius elongatus* Petr.; but as they are not, compari-
is closest with *Buthiscorpius buthiformis* Pocock, as described above, though the median eyes
ear to be almost touching one another instead of being separated by ridges as they are in that
cies (text-fig. 1). The preservation, however, is too poor for certainty on this point. The fossil is,
vever, almost twice the size of the holotype of *B. buthiformis* and considerably larger than any of
specimens attributed to that species by Pocock or by me. For convenience in description and
rence I name G.S.M. Za 2926 *Buthiscorpius major* sp. nov.

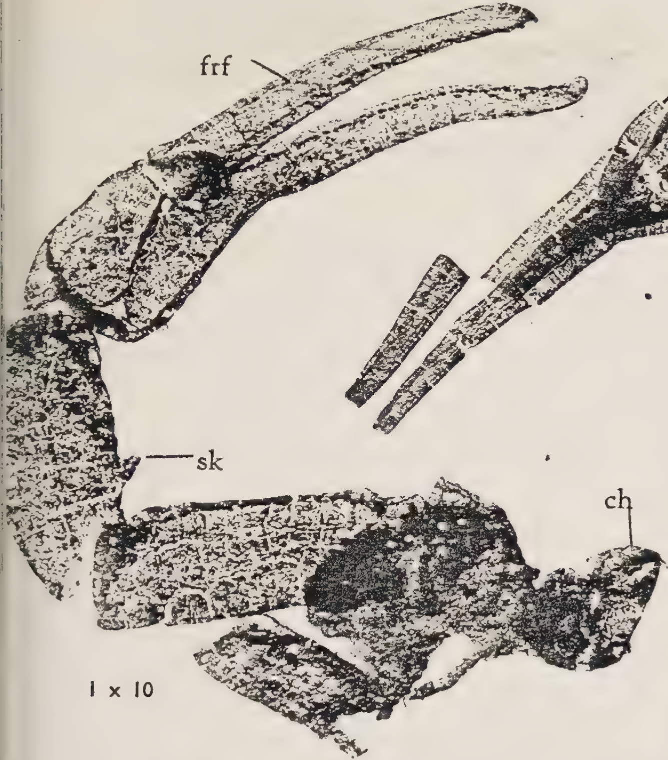
gnosis. Large Eoscorpionid 'scorpion', about twice the size of *Buthiscorpius buthi-*
mis Pocock; carapace ornamented with granules, some being large, mimicking lateral
s which are absent; median eyes small and near to one another on an eye-tubercle
hout visible ridges between the eyes; eye tubercle about two-fifths of carapace length
m the front; tergites with mucronate posterior margins; tail short and relatively
rter than in *B. buthiformis*; caudal ring XVIII not much longer than the previous one,
l shorter than the flask-shaped sting. Pedipalp hand with fingers longer in proportion
the palm than in *B. buthiformis*.

ensions. The holotype lay squashed almost flat on the ironstone. For purposes of comparison of its
ensions with those of *B. buthiformis* Pocock as described above, it must be recognized that the
ites of the present specimen are telescoped from back to front and flattened, so that the length-
ensions are relatively less and the breadth-figures relatively greater than corresponding measure-
nts in the Birmingham specimen which was fully distended lengthwise and strongly arched from
to side; and that both the above-described specimens are larger than the holotype of *B. buthiformis*
ch (without the sting) is only 22 mm. long. Making allowances for differences in preservation and
possible differences in age of the individuals, I consider it probable that the present specimen
resents an adult of a species that was about twice the size of *B. buthiformis*. Hence the specific name
or is proposed.

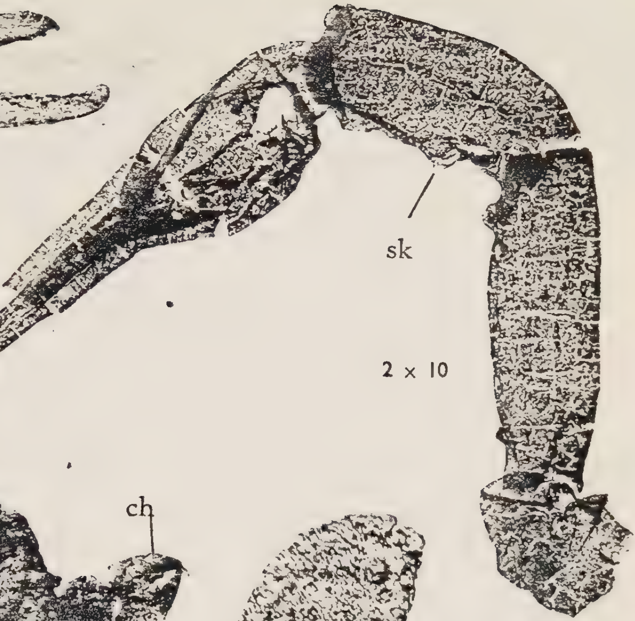
pproximate dimensions in mm. Carapace, length, 7–8; width, ? 7. Abdomen, length, 12; width
ximum at TX), 8·5; width of TXIII at front, *c.* 7, at back, *c.* 3·5. Tail, length CXIV to CXVIII, 13;
th (crushed), *c.* 3. Sting, *c.* 6. Total length, 38–40. Chelicera (hand), 2. Pedipalp, trochanter, 2; femur,
; patella, 4; palm of hand, 3·5; fingers, 4·5; total length (excluding coxa), 18·5.

scription. The body

Carapace. Pl. 51, figs. 2, 3, text-fig. 14. The exact outline of the carapace is difficult to
ke out, the sides being in places distorted or broken away. It is best seen in the 1st

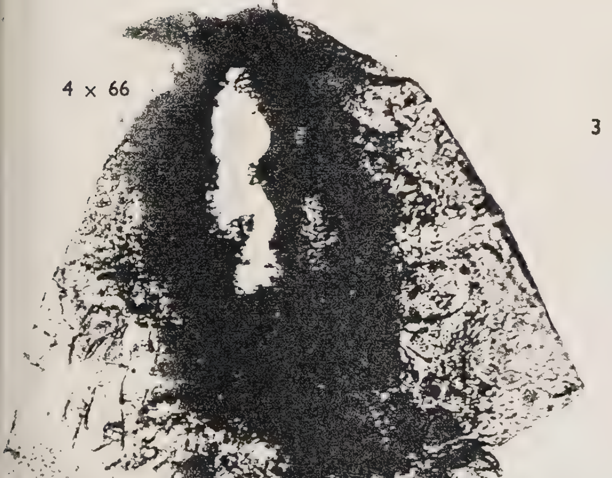


1 x 10

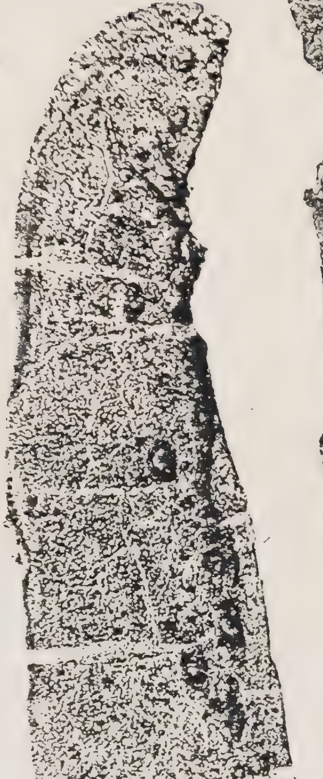


2 x 10

4 x 66



3 x 66



5 x 10

Marco-cast. It was probably almost as wide as long if allowance be made for arching, with rounded antero-lateral corners and the anterior side slightly emarginate, but it is possible that there was a median anterior triangular process, but if so it is now broken and distorted. Probably the carapace sloped sharply downwards at the front and sides. The median eyes are represented by one well preserved on the right and the other crushed. They are situated, at about one-third of the carapace-length from the front, on a slight eye-tubercle, on the hinder side of which are several large granules. The tubercle drops away behind into a forwardly bifurcating median groove flanked by two ridges which also bear granules. On the left, half-way between the eye-tubercle and the lateral margin, is a group of four or five larger granules in the form of knobs in the Marco which might be mistaken for lateral ocelli were they in the usual position. Other rather smaller knobs also occur on the antero-lateral margin. None of the knobs, however, are large enough or round enough to warrant the assumption that they are lateral eyes; for we have casts of true ones for comparison in *Compsoscorpius elongatus* Petr. (B.M. I.15862, figured by Petrunkevitch 1949, figs. 148, 150).

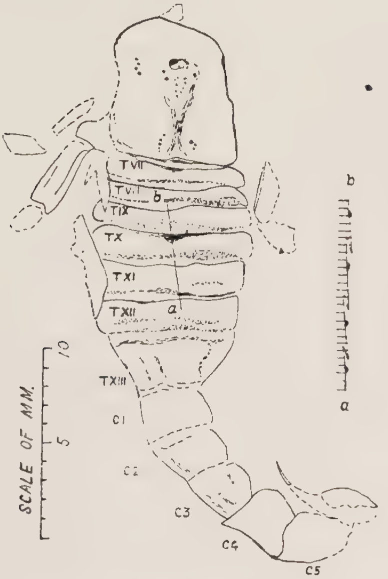


FIG. 14

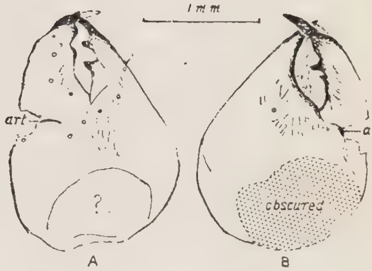


FIG. 15

TEXT-FIG. 14. *Buthiscorpius major* sp. nov. G.S.M. Za 2926. Dorsal view of dorsal surface as now visible in the two Marco-casts, with a diagram section along line *ab* to show the cast of the inside of the overlapping tergites. For key to abbreviations see p. 277.

TEXT-FIG. 15. *Buthiscorpius major* sp. nov. G.S.M. Za 2926/1. Details of L. chelicera; A, in dorsal; B, in ventral view. *art*, articulation, ? trichobothria shown as rings.

Mesosomatic tergites. Pl. 51, figs. 1–3, text-fig. 14. The general shape of the tergites is that normally found in Carboniferous 'scorpions', as fully described on p. 320. Hardly any of the chitin has survived the etching, but Pl. 51, fig. 1, shows by dark patches that it had been broken into a mosaic, as in *Lichnophthalmus* (Part 1, p. 270). There was little ornamentation except for some flat mucronate tubercles of dark-brown

ur along the posterior margins which are best seen in Pl. 51, fig. 3. Each tergite is ied by a slender linear margin at the front and sides, and by a sharp infold (doublure) nd, which can best be seen on Txi in the 2nd Marco-cast (fig. 2). The arrangement lustrated by the section AB on text-fig. 14. In Tvii–Tix there is a median depression behind the anterior margin (as there is in many Recent forms). The tergites are nected to the head in front, to the tergal plate xiii behind, and to one another by s of intersegmental skin that appear rather narrow because of the partial telescoping e segments. It will be recalled that the corresponding strips are fully exposed in the ningham specimen of *B. buthiformis* which accounts for quite a considerable increase s length (p. 286; see also p. 320). Bits of the pleural skin connecting tergites to ites and showing the linear margins are mounted on Slides Za 2926/8–/11.

etasomatic segments. Pl. 51, figs. 1–3; text-fig. 14. The tergal plate of the 1st meta-atic segment (Txiii) is imperfectly preserved, but appears to have been of the normal ring shape. Two slight ridges may represent dorsal keels on either side of the mid- but they are much less prominent than those on *B. buthiformis* (Pl. 46, fig. 2).

he caudal rings of the tail (Cxiv–xviii) appear unusually broad in relation to their th as a result of flattening and perhaps because the tail seems to have been more or turned on to its side. Some show longitudinal ridges, but little detail can be made out, where the chitin has been exposed by the etching (in 1st Marco-cast, Pl. 51, fig. 3). last ring may be imperfect, but appears to have been not much longer than the eding one and in this differs considerably from its opposite number in *B. buthiformis*.

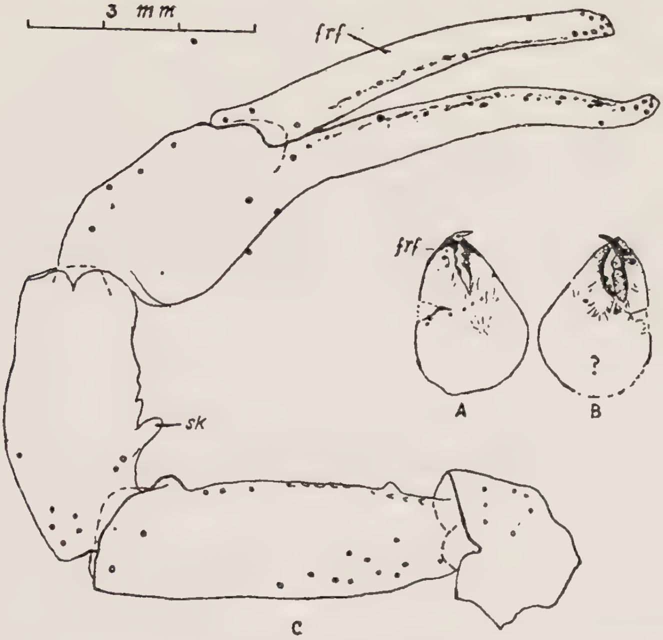
he sting was long and curved, but only the actual aculeus and a posterior portion of poison-capsule lay in the piece of rock that had been collected. These bits have been attached to the 2nd Marco-cast just as they emerged from the etching (Pl. 51, fig. 2). ext-fig. 14 the sting is indicated in the position it occupied relative to the last caudal as was determined from a comparison of the two Marco-casts.

appendages

helicerae. Pl. 52, figs. 1, 4; text-figs. 14, 15. The hand of the left chelicera is preserved ct on Slide Za 2926/1 and the broken coxal joint and bits of the right hand are bably present in Slide /2. The left hand is *c.* 2 mm. long and 1 mm. wide in the shed state. The fixed finger bears two prominent teeth on one of the two biting edges ch in life converged from the broad base of the finger to its apex. The free finger is d, the two branches closing one on either side of the fixed finger, and each carrying flattish teeth. The whole structure must have functioned as a perfect crusher, and as n has been handed down unaltered to many genera of Recent scorpions. (I have nd that the free finger is bifid in all the Recent scorpions which I have examined, but ave never seen this character mentioned in descriptions or diagnoses or shown in strations.) In Carboniferous times, as today, the chelicerae not only crushed, but ed to strain off any solid particles as the juices were sucked in, as is evidenced by a spicuous group of small setae on the sides and bases of the fingers (Pl. 52, fig. 4). re were also a few sensory bristles attached to prominent, but small, hair-bases, two he latter being visible in the photograph (*tri*). See also text-fig. 15. Recent scorpions in the same general equipment of hairs and bristles.

edipalps. Pl. 52, figs. 1–3, text-fig. 16. The two pedipalps were extracted whole and of matrix (Slides Za 2926/1 and /2). They lie neatly flattened, but curved as in life,

with the movable finger on the outside. Neither show the coxal joint, though possibly this forms part of the opaque debris that covers the trochanter and base of femur in Slide /1 (Pl. 52, fig. 1), but this is very obscure. The trochanter is short and wide; the femur has two small knobs on its inner side and displays numerous small hair-bases; the patella (tibia) is longer, with a large 'stop-knob' on its inner side (this is a conspicuous feature in many Recent scorpions), and has a few small hair-bases at its proximal end. Both femur and patella have tuberculated ribs from which the knobs project.



TEXT-FIG. 16. *Buthiscorpius major* sp. nov. G.S.M. Za 2926/1. L. chelicera and pedipalp drawn to same scale (cf. Pl. 52, fig. 1) showing distribution of granules (solid dots) and hair-bases (rings), some being ? trichobothria. The sketch does not differentiate between features on either side of the flattened skin. For key to abbreviations see p. 277.

The hand is long and slender, and nearly half the length of the whole limb (excluding the coxa). The free finger is rather more than half the total length of the hand, is not hooked at the end, and is a little shorter than the hooked fixed finger, if we measure from the apex of the angle between them. There is a conspicuous thickened process at the articulation. The biting edges are each marked by a continuous single row of granules with a number of isolated larger granules at intervals to the side of the main row. These are easily seen on the fixed finger (Pl. 52, figs. 1, 3; text-fig. 16), but I think they also occur on the free finger which has been crushed somewhat. For Recent scorpions the arrangement of granules on the pedipalp fingers is used in classification. The arrangement in Za 2926 can be closely matched with that characteristic of the Buthid genus *Anomalobuthus*, the Vejovid genera *Vejovis* and *Hadrurus*, and less closely with the Bothriurid genus *Jóphorus* (see Werner 1934, Abb. 341, 360, 361, 382).

On the great pincers there are also a few hair-bases which are almost certainly tricho-

hria scattered on the palm of the hand and at the base and tip of the fingers. Their
arent distribution is shown on text-fig. 16, but it must be recalled that it is not easy
liscriminate between organs on the two surfaces of the transparent tubular hand in
lattened state. At the tip of the fingers there are also a number of smaller hair-bases
ch may have carried ordinary small setae. The distribution and type of hair were
lently much the same as in *Mazoniscorpio* in which the actual hairs can still be seen
lace on the fragments of pedipalp mounted as B.U.721A/4, /6 (Pl. 50, fig. 3).
he general shape and proportions of the articles composing the pedipalps are similar
hose figured in outline by various authors for the following genera *Eoscorpius*, *Buthi-*
pius, *Compsoscorpius*, *Alloscorpius*, *Europhthalmus*, *Eoctonus*, and *Buthiscorpius* and
zoniscorpio as figured here; but the fingers are longer in proportion to the palm than
. buthiformis, and much longer than in *M. mazonensis*.
egs. Some fragments of legs isolated by solution were mounted as Slides Za 2926/3–
nd one bit was left in place on the 2nd Marco-cast. Most of the leg joints, however,
n the other half of the nodule which was not collected. The fragments show distinct
s or ribs, and some have a number of granules and hair-bases; but all are of little
rest since they cannot be related to particular legs, with the possible exception of
two joints on Slide /3 which appears to be the coxa and trochanter of the 3rd right
(Pl. 52, fig. 5).

Unidentifiable 'scorpion', G.S.M. Za 2924

Plates 53, 54; text-figs. 17–19

arks. This is labelled '? Scorpio, ? Shipley Clay Pit'. The horizon in the Ammanian Coal Measures
which it is said to come lies below the Top Hard Coal in the Shipley Clay Pit, near Ilkeston,
yshire.
wing to the absence or imperfect preservation of all the diagnostic parts, it is not possible to make
a generic identification of this fossil, but the sternites are not markedly lobed, and for this reason
lls into Pocock's group Orthosterni.
.S.M. Za 2924 is the much distorted, crumpled, and partly dismembered remains of a large
pion (Pl. 53, fig. 1). The length of the body, without the tail, and in its broken and crushed condi-
is about 20 mm., and the maximum width about 8 mm.; but I consider that originally the body
th was probably 27–30 mm. If this is correct—and my view is borne out by the very large size of
ppendages—the animal was half as big again as *Buthiscorpius major*. It has been preserved with an
ing or reinforcement of kaolin plus a good deal of crystalline iron pyrites on and inside many of
rgans. As a result, some of the leg segments retain their original uncrushed shape with claws and
standing out in life-like menacing attitudes (Pl. 54, figs. 4, 5), others have one joint bent sharply
on the next (Pl. 54, fig. 8), while the pecten still displays its individual teeth flexed from the plane
e rachis (like the barbs of an ostrich feather) and arranged *en echelon* along it (Pl. 54, figs. 1–3).
g across the scorpion were a number of twigs of *Asterophyllites*, also preserved uncrushed and
ning their original shapes by reason of a kaolin infilling of the pith-cavities on the outside of
h is a mere film of coaly material (Pl. 54, fig. 1). All these factors and the large size contributed
tly to the difficulty of extraction and mounting. In all, thirty-two separate mounts were made; but
najority consist of fragments, the positions of which on the body are unknown or only known in a
ral way.
wing to the flexed posture of the appendages and to distortion of the body almost every part of the
ton had been broken through when the nodule had been split open. Most of the left pedipalp,
pt the hand, lay exposed (Pl. 53, fig. 1), but during etching the only appendage extracted in any-
like its entirety was the comb of the pecten which was found completely detached from the body,
with the end of the ? 2nd L. leg lying across it (Pl. 54, figs. 2, 3). As solution of the matrix pro-
ed, various pieces of the legs appeared and were recovered, but it was almost impossible to relate

them to pieces lying at other levels. Pl. 53, fig. 2, and text-fig. 18A–C show the general shape and relative positions of the fragments at three stages and as finally interpreted. I would have been well advised to cease the development at the stage shown in the progress photograph, Pl. 53, fig. 2, but I decided to try to mount all parts in order to be able to examine them more easily and, where possible, by transmitted light or from both sides. Unfortunately, while trying to perfect the preparation containing the three sternites that are shown on the progress photograph, I dropped it. The bits that I rescued and mounted are useless. 'Striving to better, oft we mar what's well.'

There are two Marco-casts of Za 2924. The first was the outcome of the failure of the liquid plastic to adhere to the exposed surface of the fossil. The nodule was freed from this mount (first Marco-cast), and a fresh start was made. The second Marco-cast shows what was revealed after etching away the nodule, but a good deal of the chitin that had originally been exposed on the specimen had adhered to the first Marco-cast which therefore gives, on the whole, a better record of what was originally observable.

Description. Dorsal surface of Prosoma and Mesosoma

Carapace. Only about one-third of this was preserved, and since the fracture ran diagonally from the right antero-lateral almost to the left postero-lateral corner, no eyes or eye-tubercle can be seen. The margin and bordering intersegmental skin are well displayed.

Tergites. As originally exposed (Pl. 53, fig. 1) it was difficult to define the number and dimensions of the tergites, some of which, particularly TVIII and TIX, were badly twisted into a sort of hump (text-fig. 17, H). After development, however, the second Marco-cast shows six tergites increasing slightly in length from TVII to TIX, and then becoming considerably longer (as is normally the case). Part of the difficulty of interpretation appears to arise from a distension of the body, which has drawn out the usually infolded intersegmental skin (*isk* on text-fig. 17). This effect can be seen particularly well in front of

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EXPLANATION OF PLATE 53

Figs. 1–3. 'Scorpion', *indet.*, G.S.M. Za 2924. Dorsal aspect, as received; photographed under alcohol. ×3. 2, The same after etching, in ventral view, photographed under water. Impression of pedipalp on Marco-cast outlined. ×4·3. 3, Fragment of a tergite of the same. Slide Za 2924/32. ×86.

Fig. 4. 'Scorpion', *indet.* ? Metatarsus with two large spines, tibia and part of patella of ? 1st R. leg (cf. text-fig. 25). M.M. Slide L. 8194/2. ×46.

Fig. 5. '*Glyptoscorpius*', Calciferous Sandstone, Cementstone Group, Newton Farm, Foulden, Berwicks. B.M. In.25982. Structureless skin of a barbed tooth or filament on a comb which exactly matches Peach's pl. 29, fig. 17 in *Trans. Roy. Soc. Edinburgh*, vol. 30, p. 188. The irregular pattern is due to bits of adherent matrix. ×165.

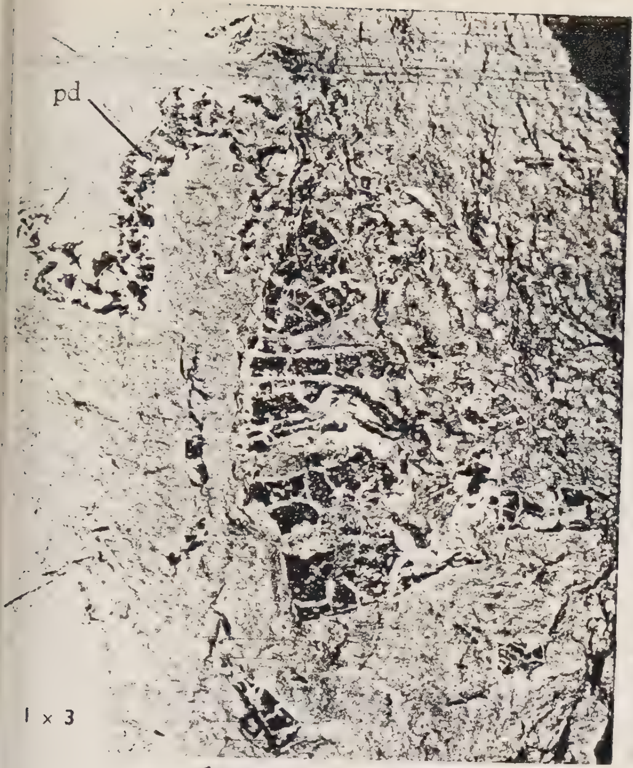
Fig. 6. '*Glyptoscorpius*', Calciferous Sandstone, Glencartholm, Dumfriesshire. B.M. In.42706. Peg-organs on an unbarbed tooth or filament of the comb. ×165.

For key to abbreviations see p. 277.

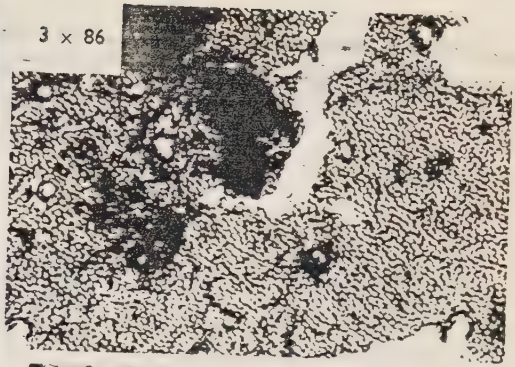
EXPLANATION OF PLATE 54

Figs. 1–9. 'Scorpion', *indet.*, G.S.M. Za 2924. 1, The ends of the two combs in ventral view, partially etched, with twigs of *Asterophyllites* lying across them. ×*c*. 4. 2, End of ? 2nd L. leg with two tarsal spurs and setae, lying across and below the crumpled L. comb; and the R. comb with a displaced tooth. Dorsal view. Slides Za 2924/1, /2. ×8. 3, Ditto, in ventral view. ×8. 4, End of 1st L. leg with the sharply flexed patella concealing part of the tibia. Slide Za 2924/6. ×8. 5, The distal part of the same to show spines on metatarsus and denticulation of the tarsal spur and claws. ×24. 6, 7, The two sides of tarsus and metatarsus of 4th L. leg with tarsal spurs. Slide Za 2924/3. ×8. 8, The tarsus, metatarsus, and part of tibia with large metatarsal spur, ? L. leg 3. The tarsal spurs not shown in this view. Slide Za 2924/4. ×8. 9, Structureless part of the chitin of a tergite with very minute hair-bases. Slide Za 2924/11. ×85.

For key to abbreviations see p. 277.



1 × 3



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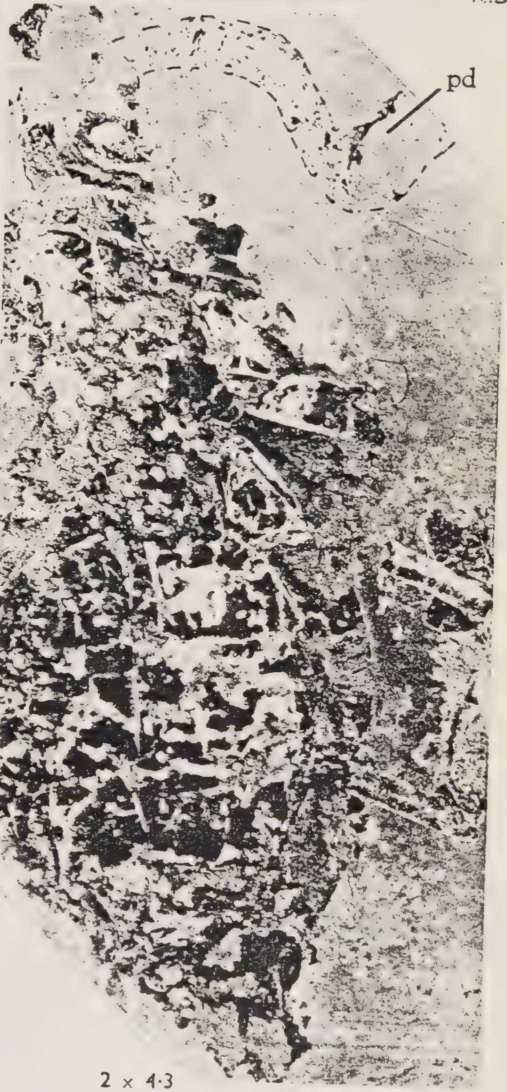
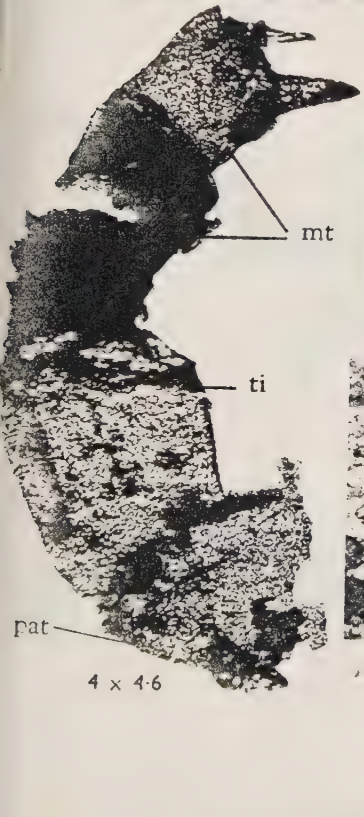
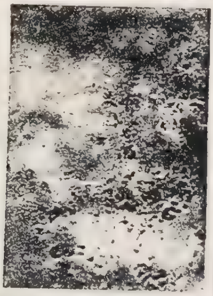


2 × 4·3



4 × 4·6



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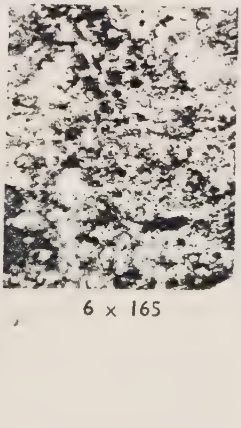
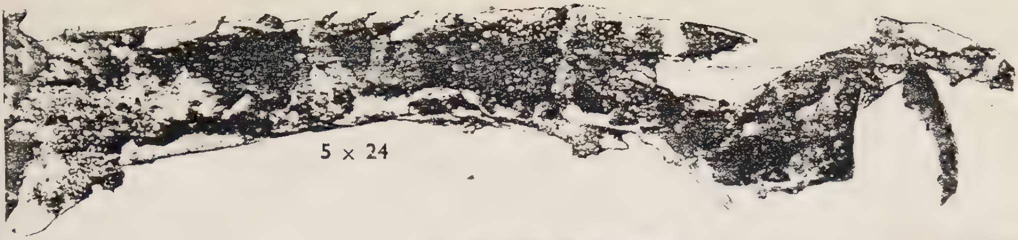
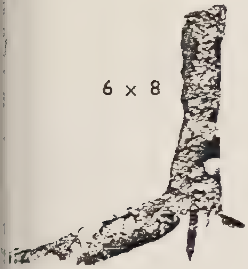


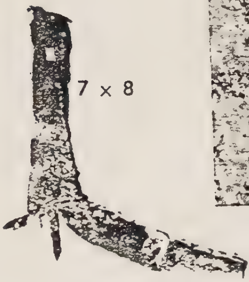
6 × 165



5 × 24



6 × 8



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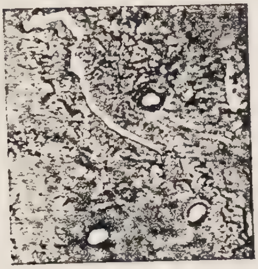
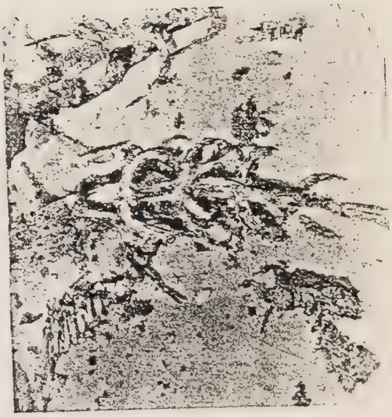
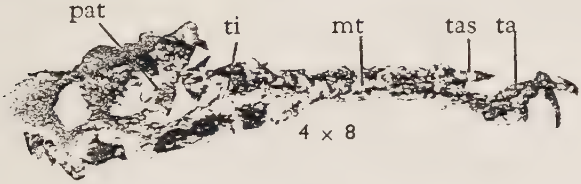


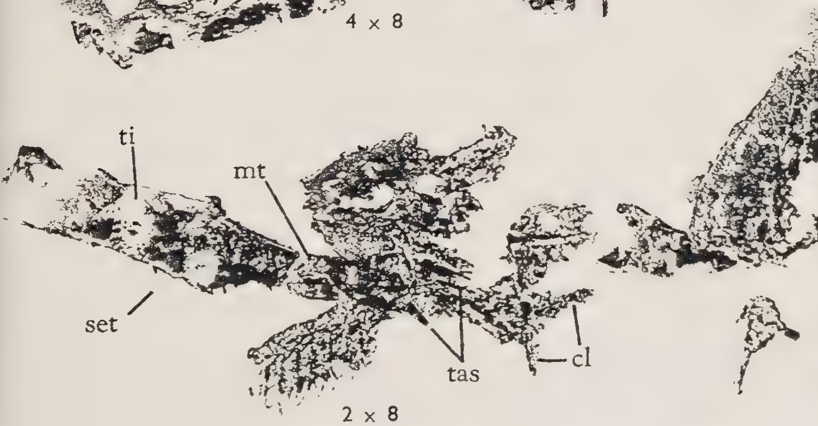
9 × 85



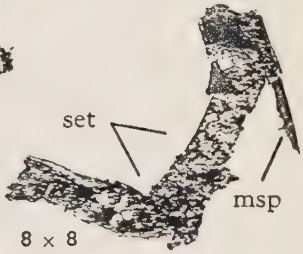
1 × c4



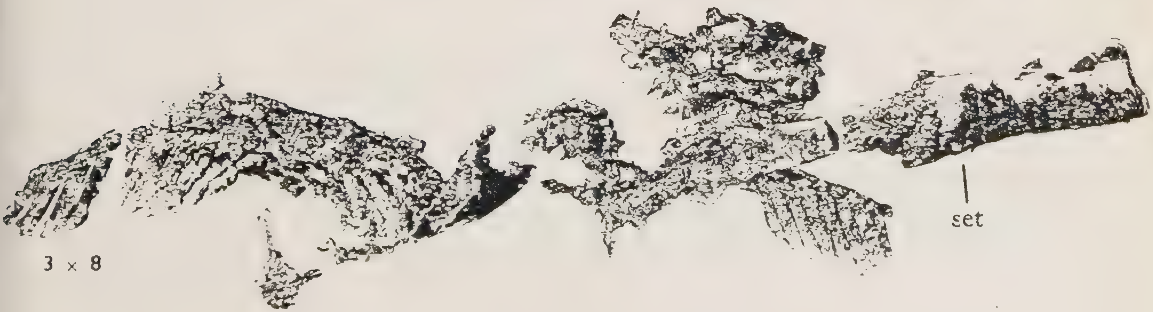
4 × 8



2 × 8

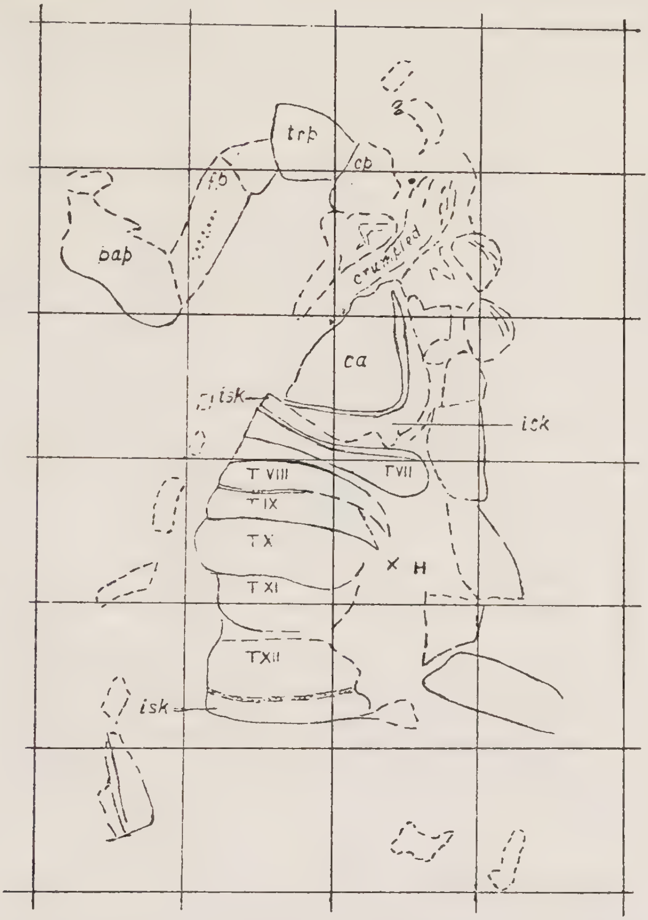


8 × 8



3 × 8

Tvii and behind Txii. The latter gives the semblance of an additional tergite (see p. 321). In Slide 31 a fragment of the posterior part of a tergite with its border (doublure) of intersegmental skin is preserved in full relief which shows the outer surface and doublure joining at an angle of nearly 90°.

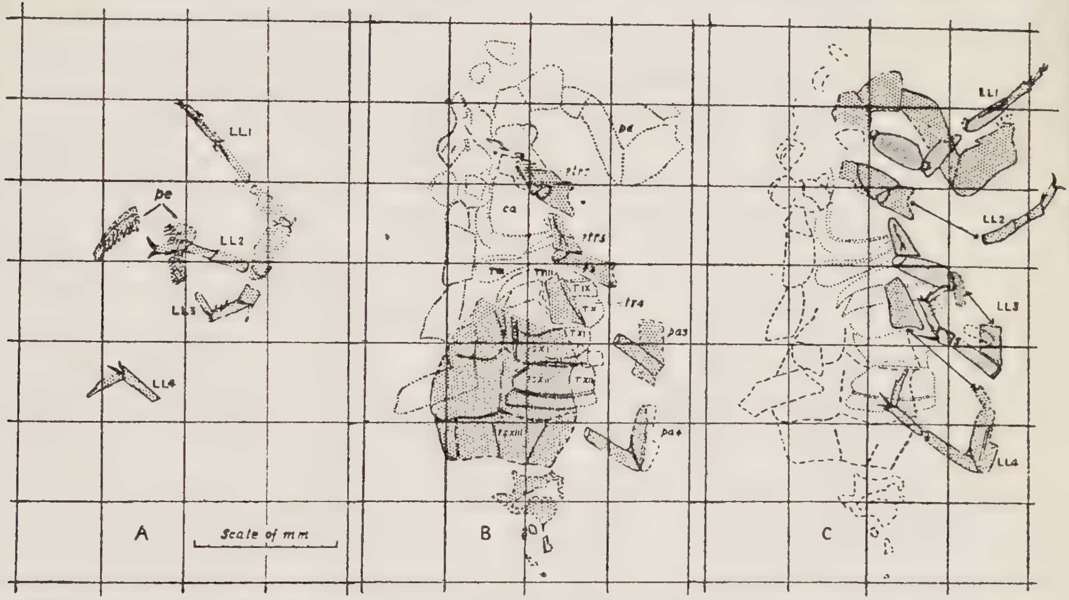


TEXT-FIG. 17. G.S.M. Za 2924. Outline of parts originally exposed or revealed on Marco-cast after etching. Grid of $\frac{1}{4}$-inch squares as on text-fig. 18. H, apex of the 'hump' of crushed tergites; *isk*, inter-segmental skin. For key to other abbreviations see p. 277.

The chitin of the tergites is well preserved in places, and a fragment mounted as Slide 32, Pl. 53, fig. 3, shows a few hair-bases on a dark-brown sheet having a distinctly cellular texture which is closely comparable with the 'reticulate structure' of a tergite of *Pareobuthus salopiensis* (Wills 1925, pl. 3, fig. 17), and of *Lichnophthalmus pulcher* (Part 1, p. 271). Elsewhere, however, bits of a very thin yellow-brown material (perhaps intersegmental skin or possibly an outer surface-film of the chitin) has adhered to the Marco-casts, which, apart from a few minute hair-bases, appears to be quite structureless (Slide 11, Pl. 54, fig. 9).

Ventral surface of Mesosoma and segment XIII

The only parts of the ventral body-skin recognized were the two sternites and ? ventral plate of segment XIII to whose unlucky fate reference has already been made, and some scraps of one or two caudal segments (Slide 18), of which nothing can be deciphered with certainty. The three ventral body-plates were fairly well exposed at one stage in the development (Pl. 53, fig. 2; text-fig. 18B). At the time I formed the opinion that they were sternites X, XI, XII, but judging from their position, as now known, in relation to the tergites (indicated on text-fig. 18B), they would appear (unless they had been displaced backwards during fossilization) to be sternites XI and XII and the ventral plate of segment XIII. Towards the middle of each plate the posterior margin appeared to be slightly notched, and the skin was folded in such a way that the development photo (Pl. 53, fig. 2) gives the impression of a median suture comparable with that on sternite X in *Pareobuthus salopiensis* (Wills 1925, fig. 2 and pl. 3, fig. 2) and *Mazoniscorpio mazonensis* (Pl. 50, fig. 2). I made a note at the time that the L. half (right in photo) of the foremost sternite was a double structure or folded on itself. Owing to the loss of the preparation all that can be stated with certainty is that none of the posterior margins were strongly lobed, but gently emarginate, that each overlapped the next one behind by an infold of the intersegmental skin, and that no stigmata occurred on the outer surface of the sternites themselves. Nothing that was seen would rule out the possibility that there were stigmata on the marginal bend-over or on the intersegmental bordering skin or doublure at the postero-lateral corners as in the Triassic scorpion *Mesophonus* (Wills



TEXT-FIG. 18. G.S.M. Za 2924. Stages in etching from the ventral side. Same grid as in text-fig. 17. A, Early stage with the combs and distal articles of the L. legs exposed. B, Final stage with ? sternites XI, XII, and sternal plate XIII, proximal parts of three legs, and patella and tibia of two. Dorsal features dotted in. C, Reconstruction. L. appendages with distal parts restored to the proximal ones; alternate appendages with fine and course stipple. Broken lines, ventral sclerites and R. leg fragments; dotted lines, dorsal sclerites. For key to abbreviations see p. 277.

1947). On the other hand, comparison with *Mazoniscorpio* appears to be so close that the two animals may well have had the same type of breathing organ.

The appendages

As the coxae (except that of the pedipalp), the sternum, and the genital operculum are missing, the relations of the appendages (including the pecten) to the body cannot be stated. Those of the right side are too poorly preserved to be identified: those of the left side appear to have been detached during burial, but without much displacement. It proved difficult to trace the connexions between the distal joints of the legs which were revealed and isolated during the early stages of etching and the proximal joints lying at lower levels. It is now clear that in most cases the intermediate joints lay in the counterpart, which was not collected. In text-fig. 18A, B, the joints of the appendages exposed at two stages of etching are shown in approximately the correct positions in relation to a common grid, and in B in relation to the dorsal organs and the left pedipalp. Text-fig. 18C is an attempted reconstruction of the L. side, with alternate appendages lightly and heavily stippled.

The *chelicerae* were very obscurely exposed and nothing was discovered about them during development.

The left *pedipalp* with the exception of most of the hand was exposed on the original surface in poor preservation, and etching revealed nothing further except strong granules on the femur. The appendage was a powerful one with the relative sizes of the joints much the same as in *Mazoniscorpio* and *Buthiscorpius major*.

The legs. Parts of all four left legs were isolated and mounted. They are almost uncrushed and in several cases have the joints sharply folded, one on the next, in the natural flexed postures of death. In many cases keels, spines, spurs, claws, and bristles project in their original shapes and positions (Pl. 54, figs. 4–8; text-figs. 18, 19B–E). One cannot fail to notice the resemblance of the fossils to the legs of dried specimens of large Recent scorpions, which is so close that it is almost unbelievable that this particular Carboniferous one was not a terrestrial animal adapted to the same general habits as its present-day descendants.

The general layout of the legs when the various parts are restored to their original positions (text-fig. 18C) appears to have been the same as in *Buthiscorpius* and *Mazoniscorpio*, namely, the anterior legs were much shorter than the posterior ones; each ended in a double claw with a pad, and each leg probably carried two tarsal spurs: the 3rd (and probably the 4th) leg had a large metatarsal spur. In addition the trochanters can be seen to have been almost pyramidal in shape (Slide 19), the tibias in some cases were ribbed and spiny, and those of the 3rd and 4th legs were very spiny at their distal ends (Slide 4, Pl. 54, fig. 8; text-fig. 19E). Several other articles also show that they too were strongly ribbed, often with short spines. The distribution of hair-bases indicates that many parts carried bristles, a number of which are preserved.

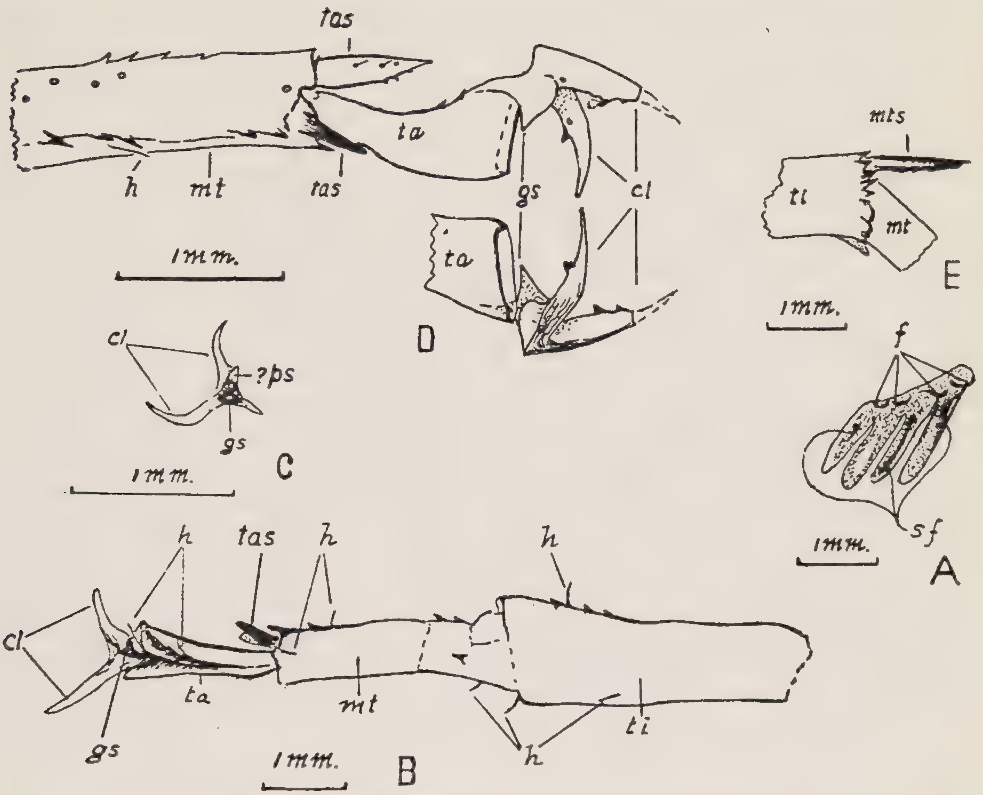
All the above features can be matched in large present-day scorpions, but there are certain minor differences in the structure of the claws and spurs.

(*a*) There are denticles along the inner edges of the claws (well seen in Slide 6 where the chitin is undamaged and unobscured by pyrites, Pl. 54, fig. 5; text-fig. 19D).

(*b*) Also there are small denticles or spines on some of the tarsal spurs and on the one metatarsal spur found (text-fig. 19E).

Both types of denticles are unknown in Recent scorpions, but occur in all the Carboniferous ones here described, except *B. buthiformis*.

(*c*) The pad (*Gehstachel*) of the claws of the ? 2nd leg (text-fig. 19c) appears to have been a conical structure not unlike the shortest type of 'dagger' in *Lichnophthalmus* (Part 1, text-fig. 8). It has a spine on one side that may correspond to one of the 'platform spines' of that genus. On the other hand, the pad on the ? 1st leg (text-fig. 19D) has no spine and in general resembles a large *Gehstachel* of a Recent scorpion.



TEXT-FIG. 19. G.S.M. Za 2924. A, Slide 2924/2. The tip of R. comb. Plain areas, kaolin; stippled, chitin. The sensory field shown where visible. B, Slide 2924/1. End of 2nd L. leg with the metatarsus restored to its original position. Note uncrushed tarsus and setae still projecting from the skin at right angles. C, Slide 2924/1. Claws and pad (*Gehstachel*) of 2nd L. leg drawn looking down on the conical pad, with a possible platford spine. D, Slide 2924/6. End of 1st L. leg, to show denticles on the two claws and on one of the tarsal spurs, and details of setae and spines. E, Slide 2924/4. Parts of tibia and metatarsus of ? 3rd L. leg, to show the spiny end of tibia and slightly denticulated metatarsal spur of triangular cross-section. For key to abbreviations see p. 277.

(*d*) There are minute sensory hairs on one of the tarsal spurs on Slide 6 while the other smaller spur seems to be quite bare. Hairs are, I believe, unknown on the spurs of Recent forms, but have been seen on spurs and/or claws in *Pareobuthus* (Wills 1925, text-fig. 3A), *Mazoniscorpio* (Pl. 50, fig. 4), G.S.M. Za 2925 (text-fig. 22), and in *Lichnophthalmus* (they are not referred to in my description in Part 1).

(*e*) This animal may have had sensory hairs on its claws, since all the forms mentioned above have them, but the tips of those extracted are either broken or heavily encrusted with pyrites, and no hairs or hair-bases can be seen.

The pecten (Pl. 54, figs. 1–3). Both combs of the pecten were preserved, detached from the rest of the body, and in a somewhat crumpled state, yet with the teeth curved and overlapping as in life. The chitin has been reinforced by kaolin which fills the inside of the teeth and preserves their original shape, but it is in many places encrusted by pyrites. One comb was partly obscured and distorted by the end of the 2nd L. leg which lay across it (Pl. 54, fig. 2). Both were slightly damaged in mounting (Slides 1, 2), but the structure of the dorsal and ventral sides are excellently shown by the several fragments, and the whole can be rearranged, as has been done on Pl. 54, figs. 2, 3.

The combs were large, each measuring at least 5 mm. in length. The rachis of each is somewhat folded and broken. It is impossible to see its shape, but the chitin of which it is composed consists of irregular polygonal areoles of thicker or darker skin, sometimes carrying a hair-base, surrounded by thinner or lighter skin. This is exactly the arrangement on parts of the rachis of *Pareobuthus* (Wills 1925), *Lichnophthalmus* (Part 1), and *Buthiscorpius* (above), and of the other Carboniferous 'scorpions' mentioned in discussing the comb of *Lichnophthalmus* in Part 1, p. 274; and it would appear to be the structure depicted by Petrunkevitch's sketches of *Eoscorpius typicus* (Petrunkevitch 1913, fig. 7) and of *Isobuthus rakovnicensis* (Petrunkevitch 1953, fig. 19). The arrangement is analogous to the papillae carrying hairs on the combs of some Recent scorpions.

The teeth are long and, being preserved in the round, appear unusually narrow when compared with others described in this paper that are crushed. At least fifteen are attached obliquely to each rachis with a row of lappet-like fulcra covering the attachment. The fulcra and teeth alternate, each of the former overlapping the two half-bases of adjacent teeth (text-fig. 19A). A sensory field of peg-organs, as described in *Lichnophthalmus* (Part 1, p. 275), can be recognized on the teeth where the chitin is unobscured by pyrites. The kaolin infilling of the teeth bears minute polygonal markings, presumably recording a cellular inner layer of chitin patterned by the nerve-endings that supplied the peg-organs. (It may, however, only reflect the microcrystalline structure of the kaolin.)

Unidentifiable 'scorpion', G.S.M. Za 2925

Plate 55; text-figs. 20–22

Remarks. This specimen, as received, bore the label '? *Anthracoscorpio*, Trowell Colliery', and the Survey catalogue states that it came from above the Kilburn Coal which is taken as the base of the Ammanian in the Nottinghamshire Coalfield.

The specimen originally showed a dorsal view of ? a fragment of the carapace, the six tergites of the mesosoma, the dorsal plate of segment XIII, and some bits of appendages of a largish scorpion, but it had been broken off obliquely so that most of the carapace and parts of the first three tergites and the whole tail had been lost. On both sides of the animal lay long fragments of some plant (Pl. 55, figs. 1, 2).

I etched it and extracted a number of pieces now mounted as Slides 1–13 (Za 2925/1–/13), but the excellent Marco-cast that I had obtained was accidently burnt. As a result there is nothing except two photographs against which the following observations can be checked. Plate 55, fig. 2, taken in air shows more clearly the segmentation, whereas fig. 1 records better the distribution of the remnants of chitin (dark patches).

Although parts of the sternites, of the pecten, and of three or four legs were etched out and mounted, and now show interesting details described below, the absence of the prosoma with the carapace, sternum, and coxae makes exact identification impossible.

Description. Dorsal surface of the abdomen

Tergites. Behind a fragment of the carapace the six tergites of the mesosoma with tergal plate xiii (Pl. 55, figs. 1, 2) measured *c.* 20 mm. in length. Each tergite was bounded by a linear anterior margin and an ill-defined posterior margin with infolded doublure (text-fig. 20). Their greatest width at Tx is about 13 mm. The last tergite and the front of the tergal plate xiii are each *c.* 10 mm. wide and the hind end of the latter is *c.* 6 mm. across. The animal had been squashed flat, and for that reason the fossil appeared to be broader than it was in life, and wider than normal in relation to its length.

Ventral surface of the abdomen

Sternites. The ventral skin had been pressed against the dorsal during fossilization, but only the impression of the linear anterior margins of the four sternites ix–xii and of the sternal plate of segment xiii are traceable on the photos (Pl. 55, fig. 2), on which text-fig. 20 has been based. Two fragments believed to be parts of sternites were recovered (Slides Za 2925/6, /10). They are made of excessively thin skin which in parts is in two superimposed sheets. One, presumably the exterior, is uniformly transparent and carries along its edge a few diminutive granules and one or two tiny hair-bases; the other is blotchy. The supposed exterior sheet has a narrow doublure (? posterior margin), where it is seen by itself in Slide Za 2925/6 (text-fig. 21A), but in the double part the doublure seems to merge into the internal sheet. To the right (in the figure) the doublure and the internal sheet appear to separate and form a possible stigma leading into the space between the sheets—an arrangement reminiscent of the stigmata on the doublure of the sternites of *Mesophonus* (Wills 1947, pp. 26–35). However, the specimen is very fragmentary and nothing reliable can be deduced from it. The same applies to the second mount (Slide Za 2925/6; text-fig. 21B) where a somewhat similar structure can be made out at both ends. It must be recalled that at the postero-lateral corners of a sternite there is a complex concertina folding of the intersegmental and interpleural skin, and it may well be that this is what we see in these two specimens.

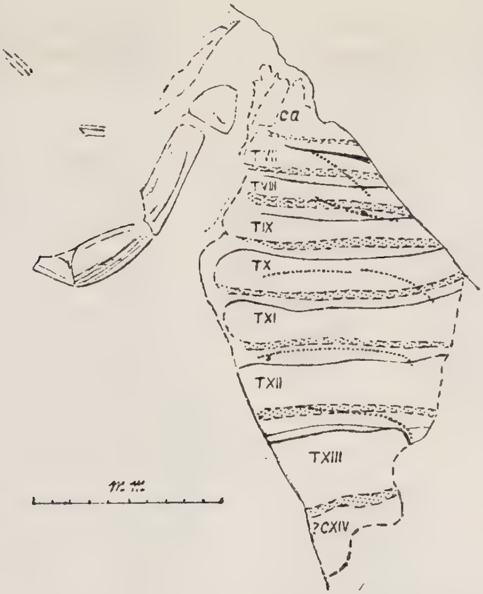
Prosomatic appendages

Legs. Parts of two legs lay exposed on the left side of the specimen as received (Pl. 55, figs. 1, 2; text-fig. 20), but it is impossible to say with certainty to which legs they belong.

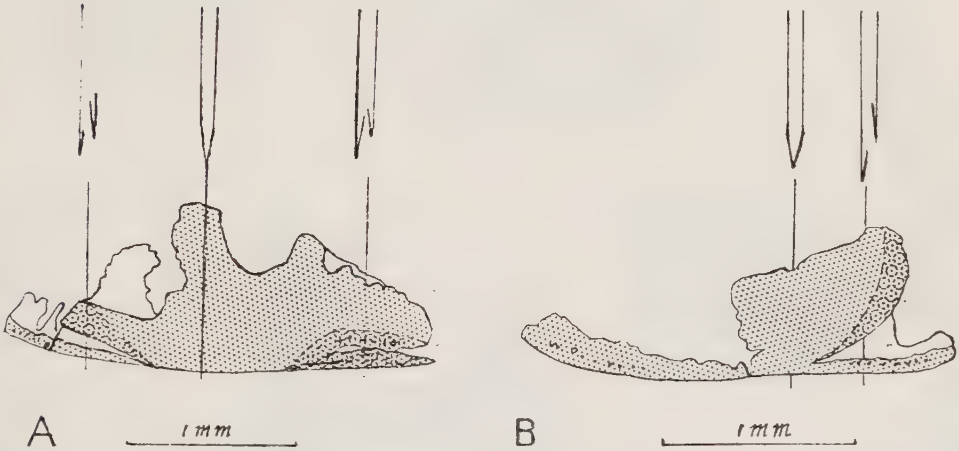
EXPLANATION OF PLATE 55

Figs. 1–9. 'Scorpion', *indet.*, G.S.M. Za 2925. 1, As received, photographed under alcohol. The dark patches are chitin. ×6·6. 2, As received, photographed in air, features accentuated in ink (cf. text-fig. 20)—continuous lines, anterior margins of tergal plates Tvii–Txiii; dotted areas, posterior marginal infolds of carapace and tergal plates; broken lines Six–Sxiii, supposed anterior margins of sternal plates. ×6·6. 3, Postero-ventral view of L. comb with rachis and teeth outlined in ink. ×20. 4, Tip of the last tooth of the comb, showing sensory field of peg-organs on one side only. Slide Za 2925/5. ×290. 5, Sensory hair (? trichobothrium) attached to hair-base, and a second hair-base on the other surface of the rachis. Slide Za 2925/5. ×290. 6, Metatarsus, tarsus and claws of 2nd or 3rd leg. Slide Za 2923/3. ×20. 7, End of tibia with metatarsal spur, metatarsus, tarsus, and claws (one detached) of ? 3rd leg. Slide Za 2925/4. ×20. 8, End of tibia with metatarsal spur, metatarsus, and tarsus with claw-lobe but minus claws; ? 4th leg. Slide Za 2925/2. ×20.

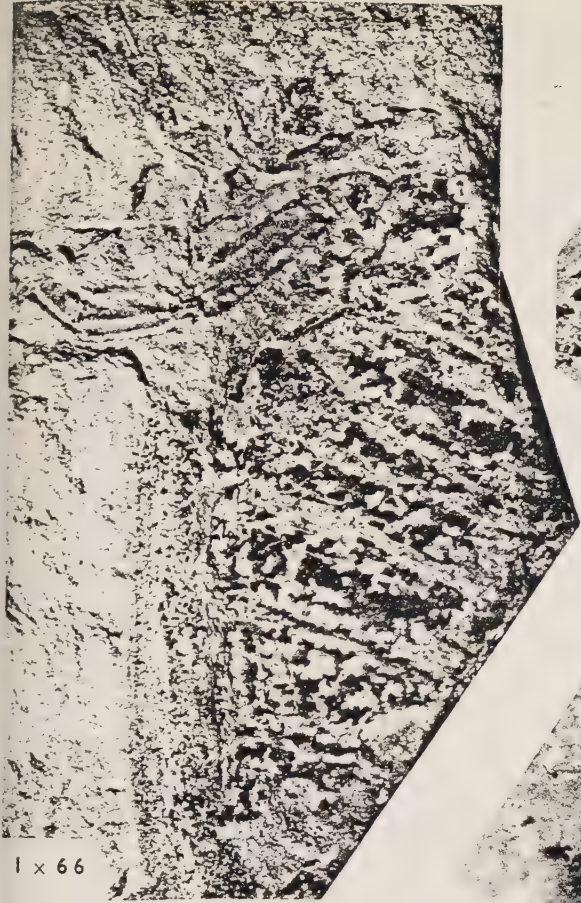
For key to abbreviations see p. 277.



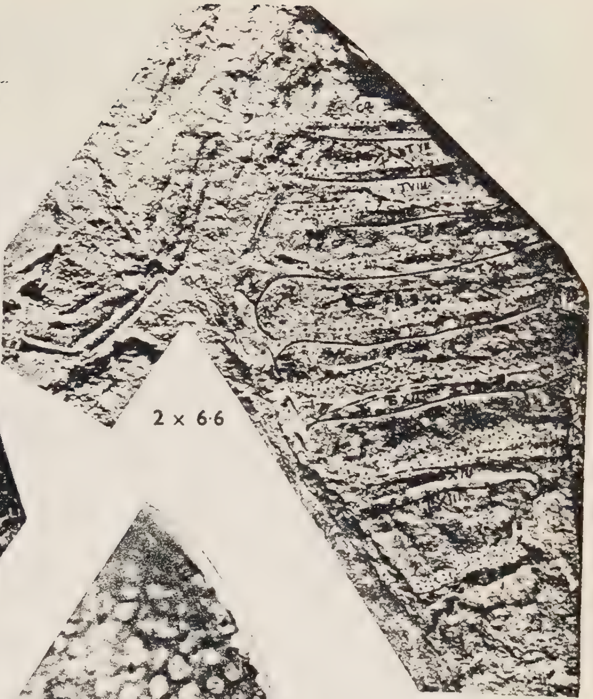
TEXT-FIG. 20. G.S.M. Za 2925, as received. The tergites defined by linear anterior margins and by posterior infolds (stippled). Impressions of the anterior margins of four sternites and sternal plate XIII indicated by dots. For key to abbreviations see p. 277.



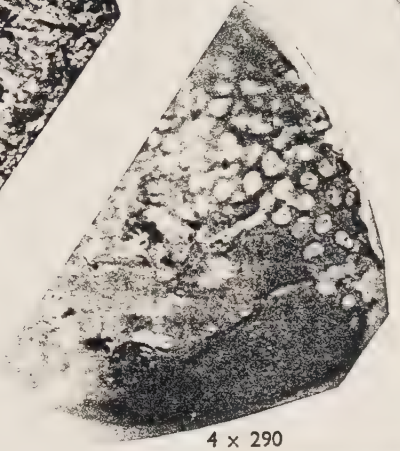
TEXT-FIG. 21. G.S.M. Za 2925. Fragments of supposed sternites in plan with tentative sections in which the upper layer, as drawn in plan, is shown to the right. Unstippled, one layer; light stipple, two layers; heavy stipple, three or four layers. A, Slide 2925/10. B, Slide 2925/6. (The long strip on the left has been restored to its original position.)



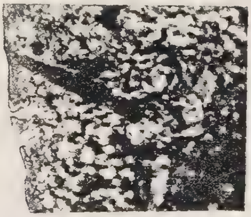
1 × 66



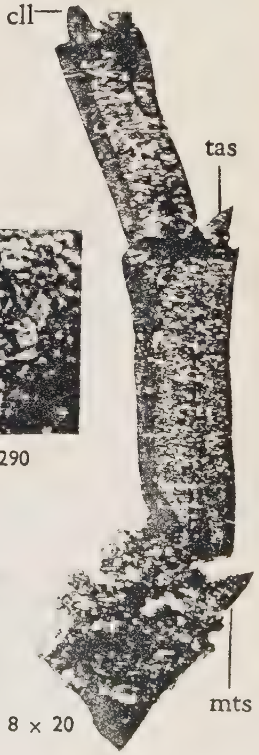
2 × 6·6



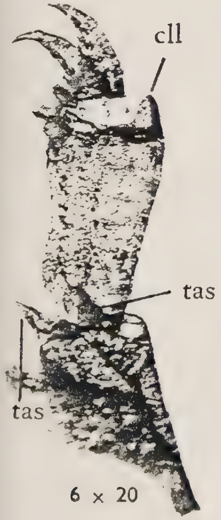
4 × 290



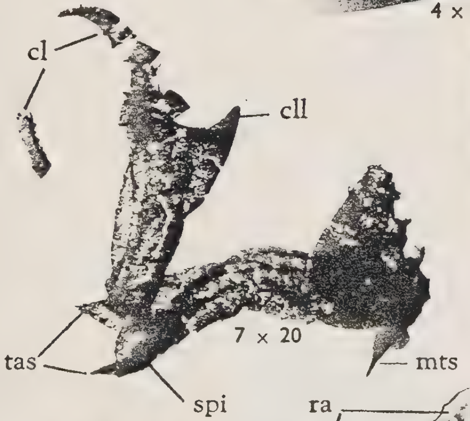
5 × 290



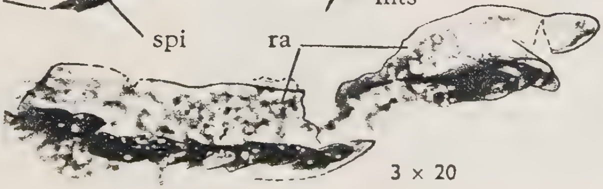
8 × 20



6 × 20



7 × 20

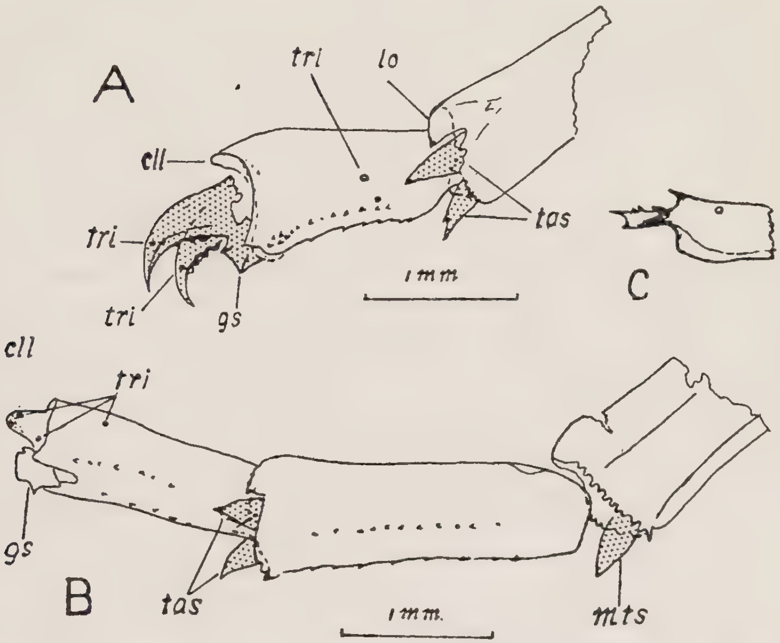


3 × 20

The hinder one shows a robust trochanter and elongated femur and patella, each with two longitudinal keels. It may be the 2nd or 3rd leg.

In the process of etching the distal ends of three legs were extracted, all with the chitinous skin transparent and virtually free from matrix—features that permit a very accurate and detailed description.

(i) The specimen on Slide Za 2925/3 probably belongs to the 2nd leg. It has been completely flattened and consequently all the parts appear wider than they were in life. The structure of the tarsus and claws, and the end of the metatarsus with its spurs are shown in perfect detail (Pl. 55, fig. 6; text-fig. 22A). The metatarsus ends in a rather spiny margin which has a distinct lobe on the outer side: on the inner side, on intersegmental skin are two tarsal spurs of which one at least has a small spine-like denticle on its side. The tarsus has two spiny ribs and two hair-bases (? trichobothria). Its outer side is produced into a prominent claw-lobe, as it is in many Recent scorpions. The leg ends in two claws, each of which is inwardly curved and sharp-pointed, with two denticulate keels that converged from the base towards the point. Near the tip each claw shows a single hair-base defined by a strong annular thickening which suggests that it carried a sensory hair (? trichobothrium). At the base of the claws is a large rather blunt pad articulated in a sinus on the inner edge of the tarsus-end, i.e. on the opposite side to the claw-lobe.



TEXT-FIG. 22. G.S.M. Za 2925. A, Slide 2925/3. Metatarsus with two tarsal spurs (one denticulate), tarsus and denticulate claws carrying ? trichobothria, and a massive pad; ? 2nd L. leg. B, Slide 2925/2. End of tibia with metatarsal spur, metatarsus with two tarsal spurs (one denticulate), tarsus with claw-lobe, and a sinus accommodating the pad (the claws were lost). C, Slide 2925/4. Spiny process on a keel of the metatarsus of 3rd or 4th L. leg; cf. Pl. 55, fig. 7, *spi*. Highly magnified. For key to other abbreviations see p. 277.

The general shape of the claws and tarsus can be matched in Recent scorpions, but the denticulation and ? trichobothria on the claws and on the spurs are traits that can, apparently, be expected on any Carboniferous 'scorpion' except those of small size.

(ii) The specimen on Slide Za 2925/2 lay farther back and nearer the body than did (i), and since it has a metatarsal spur, it is almost certainly the end of either the 3rd or 4th leg (p. 289), and in view of the length of the joints it may well be the 4th. It shows the end of the tibia and the next two articles (Pl. 55, fig. 8; text-fig. 22B). The tibia had two strong keels and ended distally in a crenulate margin. It carried a rather blunt metatarsal spur. The metatarsus had two keels marked by rows of small spines. Its distal end is less strongly crenulate than the tibia, but has two rather blunt lobes. On the adjacent connecting skin are the two tarsal spurs, one of which has distinct spine-like teeth on its edge. The tarsus also had two slight keels with spinelets and one or two hair-bases, and it shows very clearly on the outer side a fat rounded claw lobe with three hair-bases (? trichobothria). The pad of the claws is in position, but the two claws which were seen at one stage in the etching were lost.

(iii) The third specimen, on Slide Za 2925/4, Pl. 55, fig. 7, also shows a metatarsal spur, and is therefore to be regarded as the end of either the 3rd or 4th leg. It is less crushed than (i) and (ii), but the metatarsus is twisted on itself, and all three joints meet in sharp angles. Originally it lay across the body and well behind the others. Only the distal part of the tibia is preserved and this is partly obscured by matrix. At its termination, which is toothed rather than crenulate, are two sharp-pointed structures that were probably the ends of two keels. Attached to the intersegmental skin there is a strong metatarsal spur with a few spine-like teeth on its edges. The metatarsus shows two keels (? three), one on an edge and one standing out boldly in relief. Both keels carry sharp spinelets which culminate at the distal ends in sturdy spines on the margin which is also spiny elsewhere. One of the keels ends in a remarkable large spiny process sketched in text-fig. 22C. This has almost parallel sides, with spiny edges, and its end is obliquely truncated and has two terminal spinelets. It can hardly be seen in Pl. 55, fig. 7, because it is masked by one of the two tarsal spurs. So far as my experience goes it is a unique structure. The tarsus, as preserved with two or possibly three keels marked by spinelets, appears to broaden distally to end in a sharp claw-lobe carrying two or three hair-bases (? trichobothria). The apparent shape of the segment and of the lobe is the result of the crushing, and originally the latter must have resembled the corresponding organ in (ii). The claws were broken in the mounting: one is still attached and the other floated away as a tiny fragment (inset on fig. 7) which, however, shows the two rows of teeth, exactly as in (i). Each claw shows a single hair-base (? trichobothrium).

Mesosomatic appendages

The pecten. One branch of the pecten, about 4 mm. long, was etched out, but details of the rachis can only be seen in a few places owing to adherent matrix. It appears to have been small and narrow, with an oblique proximal articular end, and to have been covered with minute bristles (Pl. 55, fig. 5) attached to conspicuous hair-bases that were in some cases sited on areoles of darker skin. No subdivision of the rachis can be seen. Along one side is a row of at least seventeen overlapping teeth attached obliquely to the rachis, the last of these being the terminal one. The teeth stand out with intervening spaces in a remarkable way which is easily seen with a binocular microscope, but are

difficult to photograph (Pl. 55, fig. 3). Each tooth has on one side a sensory field covered with minute thin-skinned circles (Pl. 55, fig. 4). Even with a high-power objective I cannot be certain that a papilla or peg occurs at the centre of any of these, but it is probable that there was originally one in each, as in the other examples described.

Unidentifiable 'scorpion', M.M. L.8194

Plate 53, fig. 4; Plate 56, fig. 1; text-figs. 23–25

Occurrence. Coal Measures, probably about 100 feet above the Arley Mine Coal, *Communis* Zone, Sparth Bottoms, near Rochdale, Lancashire.

Remarks. This specimen, as received, showed the abdomen and one—probably the last—caudal segment of a diminutive 'scorpion'. It consisted of two parts that had been glued together. The crack is seen in Pl. 56, fig. 1, and in text-fig. 23. In the hope of discovering the structure of the prosoma the two pieces were separated and the smaller anterior portion with the remains of tergites VII to IX and some leg segments, and (as proved later) one chelicera was treated with shellac to hold the exposed parts together. This treatment proved a mistake, because the shellac was affected by the hot HCl and also was not a strong enough support. The other portion was embedded in plastic, etched in the usual way, and can now be studied from both sides of a Marco-block, but it is by no means an easy specimen to interpret because there is very little chitin preserved, and because the dorsal and ventral skins have been somewhat displaced laterally and then have been pressed tightly together with virtually no intervening matrix. Consequently impressions of sternites appear in the dorsal aspect and of tergites in the ventral. On the R. side the ends of two or three sternites are folded over on to the dorsal surface with the result that the tergites are here sandwiched between two layers of sternite (+pleural skin). See text-fig. 23B. It is hardly surprising that little can be learnt from the specimen about the nature of the creature's respiratory organs.

In the absence of the carapace, the coxo-sternal region, and pincers it is impossible to identify the genus or species of this tiny 'scorpion', but nothing has been found that would preclude it from being assigned to the Eoscorpioniidae.

Dimensions. M.M. L.8194 is part of the smallest of all the Carboniferous 'scorpions' that I have developed. It is preserved with the body extended, but even so the six tergites (TVII–TXII) and the tergal plate XIII only measure 8 mm. in length, to which must be added another 8 mm. for the tail (to the supposed last caudal ring). Allowing 2·5 to 3 mm. for the carapace and 1·5 mm. for the sting, I estimate the whole animal was 23–24 mm. long, but the tergites are all separated from one another by strips of intersegmental skin that make up about half the 8 mm. length, stated above. (The specimen provides a fine example of the difficulty of counting the number of tergites in a poorly preserved 'scorpion', see also p. 321.) The width of tergite XII, which appears to be the widest, is in its flattened state about 3·5 mm.

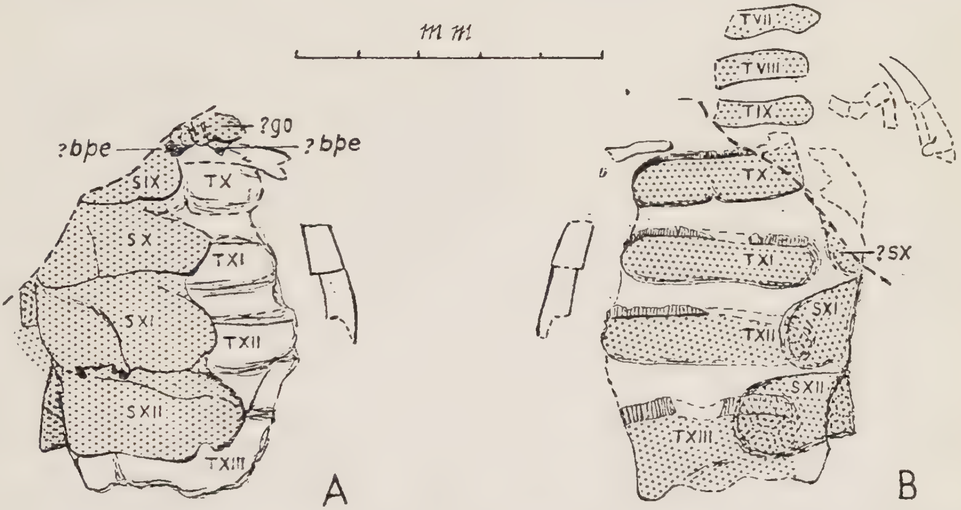
The chitin of the tergites and appendages has a curious pustulose appearance due to a pronounced cellular texture (Pl. 53, fig. 4), and is penetrated by frequent pore canals. It can be compared with that to be seen in *Spongiophonus* (Wills 1947, p. 2, pl. 9, figs. 8, 13), though the cell-walls are less regular.

Description. Dorsal surface of the abdomen

Tergites VII–XII and tergal plate XIII (Pl. 56, fig. 1; text-fig. 23B). Before the anterior section of the specimen was removed it showed parts of three short anterior tergites (VII–IX); but these, with the exception of tiny fragments (Slides L8194/6, /?3), were lost during preparation. The tergites show as dark stripes on Pl. 56, fig. 1, which was photographed before etching. In the Marco-block tergites X–XII and tergal plate XIII together with the intersegmental skin can be examined in detail. The tergites themselves are seen to be defined by linear anterior margins of thickened skin. The posterior margins are poorly preserved; but in each case there is a distinct ridge visible in oblique lighting,

which represents the position of the posterior marginal fold along which the intersegmental skin could be turned in under the tergite when the animal was not distended (see p. 320). The tergites are progressively longer from Tvii to Txii and, as mentioned above, the strips of intersegmental skin are almost as long as the tergites which they separate.

The R. ends of Txii and Txiii appear to have been partially concealed by the bending over of the ends of sternites xi and xii. Txiii is poorly preserved, but its anterior margin seems to be a thick line of dark chitin. The posterior margin would appear to be abnormally wide, but I may have been misled in interpreting this crushed and defective part of the fossil.



TEXT-FIG. 23. Manchester Museum L8194. A, Ventral aspect of abdomen. B, Dorsal ditto. The heavy broken line defines the original fracture. ? *bpe*, possible bases of combs. For key to other abbreviations see p. 277.

Ventral surface of the abdomen

Sternites, text-fig. 23A, B. The sternites lie firmly pressed against the inside of the tergites, but they can be examined by reflected light on the ventral surface of the Marcocast. They are unlobed, roughly rectangular plates, longer than the corresponding tergites, with their lateral ends distinctly rounded. Here and there can be seen fragments of the linear anterior margins. There is probably a median suture in Sx (as there is in *Mazoniscorpio*, p. 298), but the appearance of one on Sxi is, I think, due to a fold or to the impression of the right end of the sternite where it has been turned over on to the dorsal surface (compare text-fig. 23A and B). Sxi has on the median section of its posterior margin several large mucrones. The true L. ends of Six and Sx can be seen to overhang at the postero-lateral corners, suggesting that there was a deep doublure and pouch as in *Mazoniscorpio* (p. 299). Since there is no sign of any stigmata on the exposed surface of the sternites, the above-mentioned pouches may have been connected with respiration, as has been argued above (pp. 299, 300).

It is difficult to say whether these ventral plates are sternites ix–xii or sternites x–xii and sternal plate xiii. I favour the former explanation and consider that the three hinder plates are somewhat displaced backwards on the L. side, so that Sxii lies partly below

the tergal plate, Txiii. The displacement is effected by the widening out of the intersegmental skin behind the L. postero-lateral angles of the sternites.

Caudal segments. Only the supposed last caudal segment is preserved attached to the Marco-cast. It is badly preserved, but seems to have been the usual cylinder reinforced by two or more keels.

Appendages of the Prosoma

Only isolated fragments were recovered in preparing the anterior part of the specimen.

Chelicera, Slide L8194/1, text-fig. 24. This tiny specimen shows one of the fingers of a chelicera, and because it is not bifid I incline to the view that it is the fixed one. However, the part of the specimen where the palm of the hand should be found is obscured by matrix. The finger itself is about 0·4 mm. long and shaped like the beak of a parrot. From its sharp point descend two biting edges which diverge towards the base. Near here are two blunt denticles on one edge: the other carries nearer the point a single sharp spine of which only the tip is visible. Under a $\frac{1}{4}$-in. objective this latter can be seen to have three hair-like spines projecting from its sides (text-fig. 24, inset).

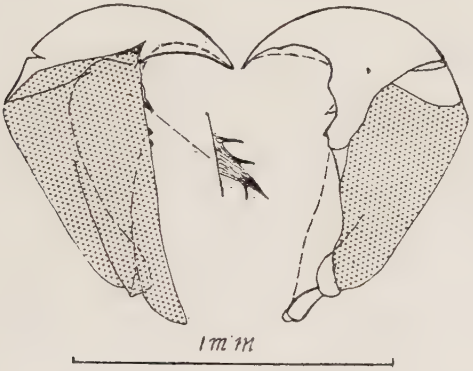


FIG. 24

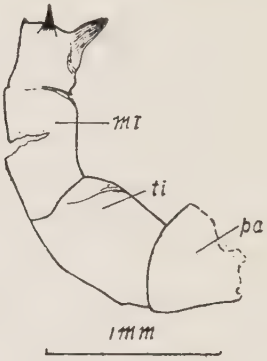


FIG. 25

TEXT-FIG. 24. Manchester Museum L8194/1. Two aspects of the chelicera with an enlargement of a spine with three spinules. Stippled areas are partly concealed by matrix.

TEXT-FIG. 25. Manchester Museum L8194/2. Probably part of the 1st R. leg, in ventral aspect. For key to abbreviations see p. 277.

A walking leg, Slide L8194/2, text-fig. 25. As this small specimen is almost free from any matrix, the two apposed layers of chitin are transparent and show the cellular structure noted above. Parts of three joints (the four-jointed appearance is due to a fold across the metatarsus) are preserved, which I interpret as patella (fragment only), tibia, and metatarsus, the last ending in one very large and two smaller spines, each being an outgrowth of the metatarsus and not a movable spur. The specimen measures less than 2 mm. and, by virtue of its small size and distinctive shape, is probably part of the first leg.

Other unidentifiable fragments from the prosoma are mounted on Slides L8194/3, /6.

WATTISONIA gen. nov.

Type species *W. coseleyensis* sp. nov.

Diagnosis. A 'scorpion' with large tergal plate xiii covered with numerous granules, the larger ones ranged along two low dorsal keels. Sternal plate xiii much larger than the

tergal, and apparently possessing a median sinus in its posterior margin where a low median keel ended; anterior margin linear, and crossed by a short median line from which the median keel runs to the supposed posterior sinus.

Wattisonia coseleyensis sp. nov.

Plate 56, figs. 2–4; text-figs. 26, 27

Holotype. B.U.722A, B, and Slides W2A/1, /3; W2/2. Almost certainly from the Ten-foot Measures above the Thick Coal, Coseley, South Staffordshire.

Remarks. This small specimen lies in two half-nodules collected by Mr. J. T. Wattison of Shrewsbury many years ago, and generously presented to me for development. The two halves lie embedded in two Marco-blocks which bear the labels I originally gave them, namely W2 and W2/A on 722B and 722A respectively. Only five tergites and the tergal plate of segment XIII were exposed in dorsal view in 722B and in ventral view in 722A. As etching proceeded, 722A revealed nothing fresh except the L. end of sternal plate XIII which had been bent over on to the dorsal side (Pl. 56, fig. 2). This was detached and mounted as Slide W2A/1 (Pl. 56, fig. 4). Part of TVIII also floated free and was mounted as Slide W2A/3 (Pl. 56, fig. 3). The embedded sclerites are now completely transparent and display in B.U.722A better than in any other specimen that I have developed how the tergites articulated with one another and how the 'scorpion' could distend itself.

B.U.722B, on etching, revealed the downturned ends of the tergites, especially the R. ends, part of which broke away and was mounted as Slide W2/2. Also the remaining two-thirds of SXIII which had not been bent over dorsally was exposed. This part is not fully transparent, but it is beautifully preserved. The shape of SXIII appears to be unique, and for this reason I propose to name this 'scorpion'-fragment *Wattisonia coseleyensis* in honour to its discoverer.

I was misled during the etching of both specimens by a laminate structure carrying minute hairs on one side into thinking that I had found a detached sternite, but close examination later showed it to be part of a pinnule of ? *Neuropteris*. A part was mounted as W2A/4 and /5.

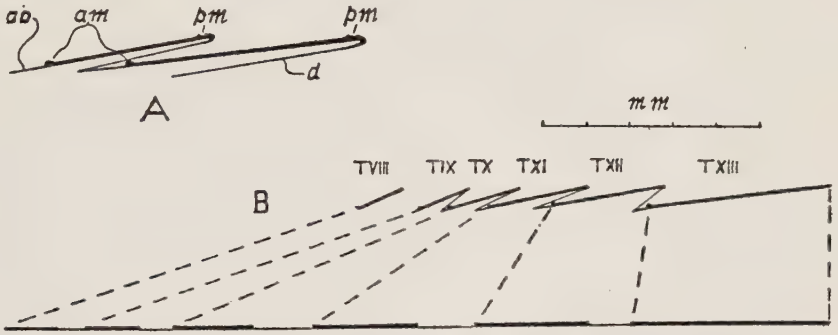
Diagnosis. As for the genus with the following addition; small 'scorpion' with normal, rather hairy tergites. Sternal plate XIII thickly coated by posteriorly directed setae attached to small hair-bases. All other organs unknown.

Description. Dorsal surface

Tergites. Parts of the chitinous skin of tergites VIII–XII occur in both specimens as a result of their complex structure which is best revealed in the external aspect etched out in B.U.722A (Pl. 56, fig. 2) and in a fragment of TVIII mounted as W2A/3 (Pl. 56, fig. 3). As these specimens throw light on the normal structure of the dorsum of Carboniferous 'scorpions' I describe them here in detail. From them it can be proved that each tergal sclerite consists of the external skin of the tergite proper covered with scattered hair-bases, and defined in front by a linear anterior margin which curves round at each end into linear lateral margins. These disappear behind, where the posterior margin, defined by a line of minute granules and hair-bases, begins. This margin is really part of an extensible infold by which the external surface passes into the inturned posterior border or doublure. The chitin of the latter was doubtless very thin, and only in one or two places can it be proved to exist in this fossil. In several specimens that I have developed, this posterior infold, filled with the Marco, has been revealed by the etching. It is probably responsible for the rather indefinite, often wide, distinctive strips that indicate the

posterior sides of the tergites when they are exposed in dorsal aspect on the unetched surface of a nodule (Pl. 51, figs. 1–3; Pl. 55, figs. 1, 2). Reverting to *Wattisonia*, in front of the anterior margin is the anterior border, which in a forward tergite may be half as long as the external surface of the tergite itself (Pl. 56, fig. 3), but which is probably relatively shorter on the hinder ones compared with the greater length of the sclerites. The anterior border carries a line of hair-bases just in front of the anterior margin (a similar line of actual hairs can be seen in *Benniescorpio tuberculatus* (Peach), text-fig. 28). Outside the linear lateral margin is the lateral border of pleural skin which also carries hair-bases.

The specimens show that when the 'scorpion' was in a contracted posture, the anterior border, the anterior margin, and the front half of the external skin of one tergite were covered by the external skin of the preceding tergite. It follows that the doublure of the latter must have stretched forward internally to join the anterior border of the underlying tergite (see text-fig. 26A); but this union is nowhere visible, probably by reason of the extreme tenuity of the chitin. Flattened as all these parts are, except the posterior marginal fold, the area of overlap consists of three layers—the external surface plus doublure of one tergite overlying the front end of the external surface and the anterior border of the next behind. Parts of several such areas show as dark strips on Tix–xii (Pl. 56, fig. 2). It will be noticed that they are much broader than the lighter intervening strips where only the external skin is present, except in the case of Txii in which the overlap on to Txiii was quite small. In a poorly preserved specimen the three-layer strips might easily be mistaken for whole tergites, each apparently showing its own



TEXT-FIG. 26. *Wattisonia coseleyensis* gen. et sp. nov. B.U.722A. The structure and method of expansion of the dorsum. A, Section through two complete tergites (reconstruction). *ab*, anterior border; *am*, anterior linear margin; *d* posterior border or doublure; *pm*, posterior margin with granules. B, Diagram section to scale through L. side of the contracted body (Tviii shown slightly displaced as in the specimen. C, Ditto, with the intersegmental skin and tergites fully extended.

EXPLANATION OF PLATE 56

Fig. 1. 'Scorpion', *indet.*, M.M. L.8194. As received. ×6.

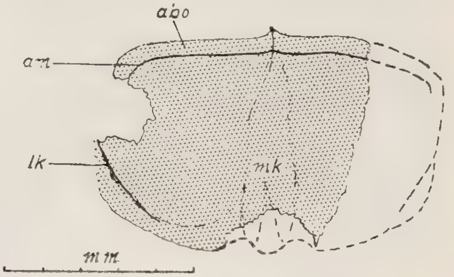
Figs. 2–4. *Wattisonia coseleyensis* gen. et sp. nov. 2, Dorsal view of dorsal surface with part of Sxiii, after etching (some features accentuated in ink). B.U.722A. ×6. 3, End of ? Tviii or Tix. Slide 722A/3. ×24. 4, Setae on Sxiii. Slide 722A/1. ×70.

Fig. 5. *Benniescorpio tuberculatus* (Peach). Supposed Sxi (cf. text-fig. 28), G.S.M.E. 9675. ×12.

For key to abbreviations see p. 277.

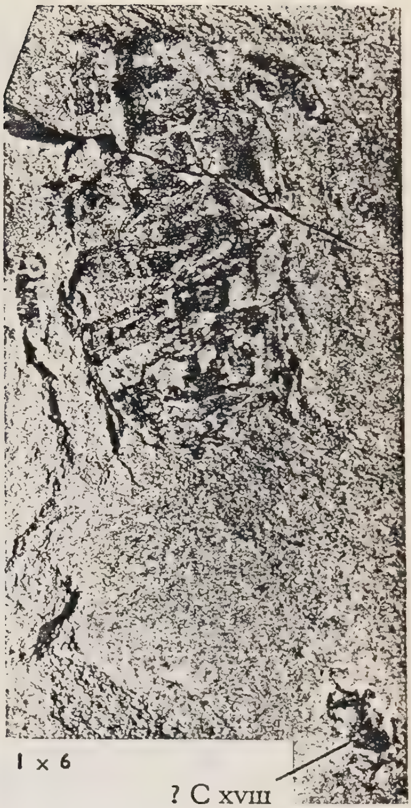
anterior margin; but, as pointed out above, the margin that can be seen really belongs to the next segment behind.

Tergite vii is missing. The others increase in length from Tviii to Txii (see text-fig. 26c), and in the amount of overlap from Tviii to Txi. Nearly half of each tergite is overlapped by the next one in front. The overlapping of the tergites implies a potential increase in the length of the mesosoma (on distension) that has long been postulated to explain the overlapping of the ventral sternites in Carboniferous ‘scorpions’. The dorsal overlap has been noted above in several cases, but this specimen shows very clearly the enormous amount of increase that was possible. On text-fig. 26b I have plotted to scale a diagrammatic section of the L. side of 722A, and text-fig. 26c shows the same with the skin fully extended (a condition doubtless never attained in life). The lengths of the anterior borders and adjacent posterior doublures are minimal. It turns out that at the maximum extension the length from the front of Tviii to the back of Txii was doubled. In the past a want of appreciation of this feature may have led to misinterpretation of poorly preserved specimens; and in this connexion it would be interesting to etch out the type specimen of *Mazonia woodiana* Meek and Worthen to determine whether the supposed seventh mesosomatic tergite exists or whether the intersegmental skin between the carapace and the first tergite has been misinterpreted as an extra tergite. I have examined a good cast of the holotype, and I am inclined to think that this second alternative is the explanation of the supposed abnormality which was questioned long ago by Scudder in Zittel (Eastman's edition), as pointed out by Woodward (*Geol. Mag.* **44**, p. 544). If the extra tergite should prove to be fictional, another of Petrunkevitch's (1955, p. P70) superfamilies and families would disappear. (Also his whole suborder Protoscorpionina is based on the Carboniferous *Mazonia woodiana* and on the Silurian genera *Palaeophonus*, *Dolichophonus*, and *Proscorpius*, which three, he states, have the first tergite (of the supposed seven characterizing his suborder) concealed under the carapace. None, however, of the published figures of these three forms shows more than six mesosomatic tergites, and the transverse mark across the hinder part of the carapace, which is the sole evidence for his statement about the concealed tergite, can be matched in many Recent scorpions and probably in Carboniferous ones also (p. 285). I therefore regard as ill-founded his 1955 diagnosis of the family Palaeophonidae ‘First abdominal tergite concealed under carapace, its anterior edge indicated by a transverse furrow’.)



TEXT-FIG. 27. *Wattisonia coseleyensis* gen. et sp. nov. B.U.722B. Sternal plate xiii. Stippled part is preserved in Marco-block W2. *abo*, anterior border; *am*, anterior margin; *lk*, lateral keel; *mk*, median keel.

Tergal plate Txiii of *Wattisonia* is imperfectly preserved. What remains of its anterior border suggests that it was only to a small extent overlapped by Txii. This would imply that this articulation did not play a large part in the distension. Txiii appears to taper backwards more slowly than is usual, but it has the normal semi-annular posterior margin with a narrow doublure. Its surface is devoid of hairs and hair-bases, but is ornamented with numerous, circular granules, the larger of which lie along the two dorsal keels (cf. *Buthiscorpius* and *Mazoniscorpio*).



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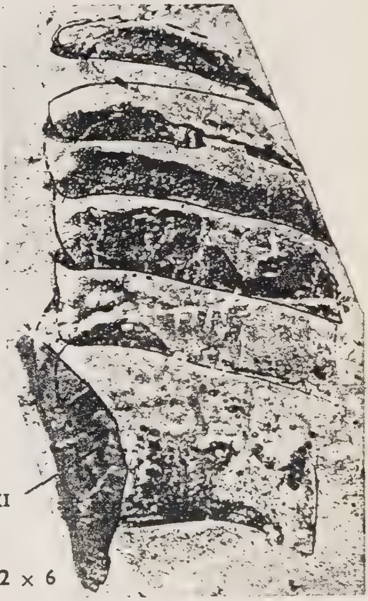

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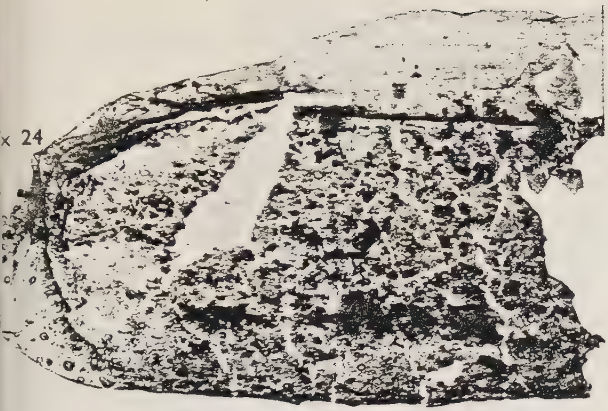

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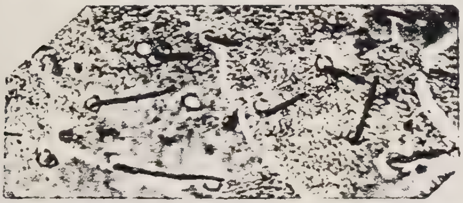

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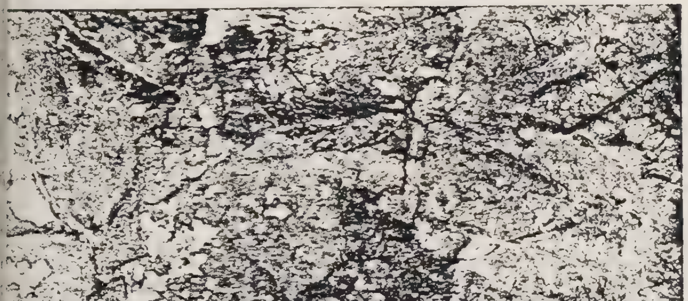
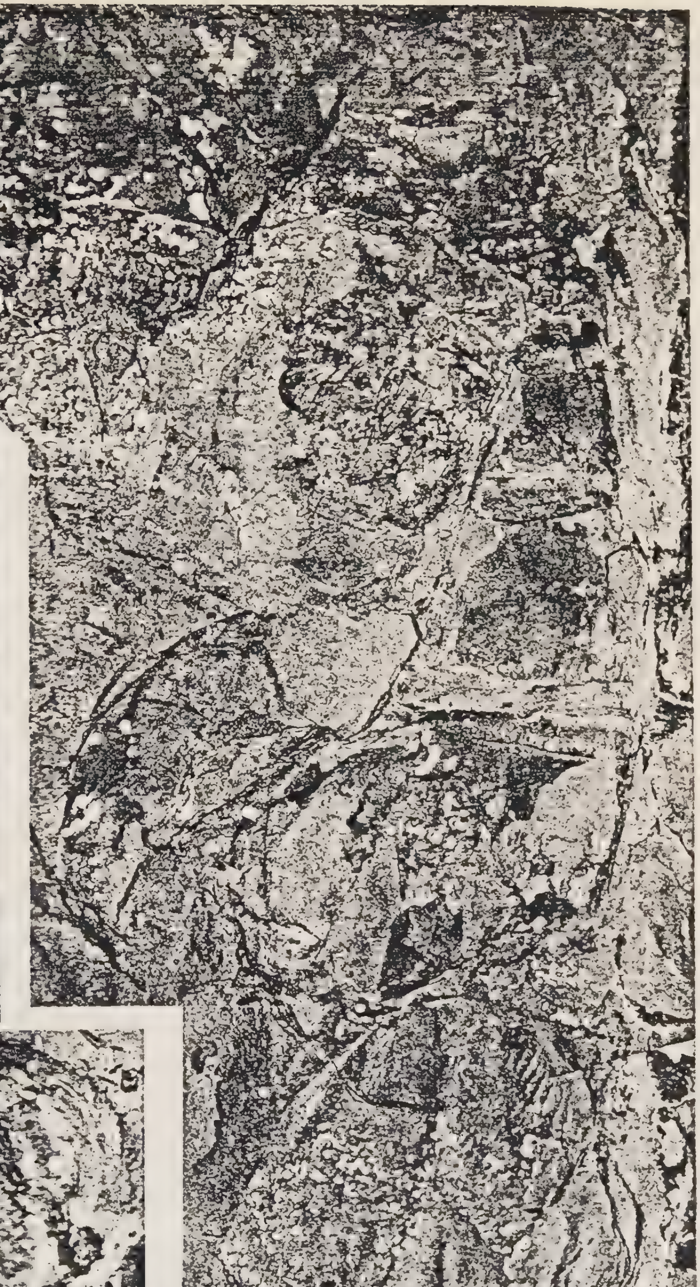
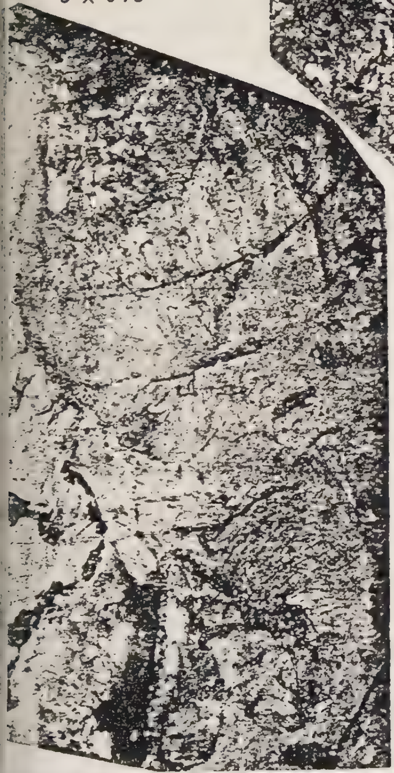


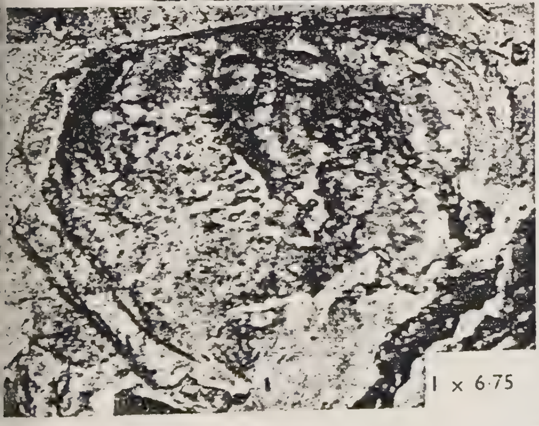
× 12

2 × 6·75



3 × 6·75





1 × 6·75

322–323

Ventral surface

Sternal plate XIII. No ventral organs were discovered except the sternal plate of segment XIII, the structure of which appears to be unique; but it must be pointed out that the corresponding plate in all the forms here described is in no case satisfactorily displayed for comparison. About two-thirds of it lies semi-transparent in the Marco-block B.U.722B, the rest, shown in the progress photo of 722A (Pl. 56, fig. 2), as it etched out, is mounted as Slide W2A/1 (Pl. 56, fig. 4).

In its flattened state SXIII is much wider than TXIII, implying that in life it was strongly arched downwards. It cannot be satisfactorily photographed, but is drawn in text-fig. 27. It appears to have been defined at the sides by two lateral keels, the R. one of which can be seen on the left side of 722B. In front it is defined by a linear anterior margin with a narrow anterior border carrying a line of hairs. Across the middle of this margin is a short thin line—probably a sharp fold of the skin—which is continued backwards as a low median ridge that widens towards what appears to be a median sinus in the posterior margin. The ridge was a median keel ending perhaps in a blunt spike, and the sinus may not be original, but the result of the fracture and flattening of the keel and posterior margin. The whole surface of the sternal plate is thickly coated with rather long setae, many of which are still attached to their hair-bases (Pl. 56, fig. 4).

SUPPLEMENT TO PART 1

LOBOSTERNI Pocock 1911

BENNIESCORPIO gen. nov.

Type species *Eoscorpius tuberculatus* Peach

Benniescorpio tuberculatus (Peach)

Plate 56, fig. 5; Plate 57; text-figs. 28, 29

Eoscorpius tuberculatus Peach 1881, p. 398, pl. 23, figs. 8, 8*a*, 8*d*, 8*e*.
Centromachus tuberculatus Thorell and Lindström 1885, p. 25.
Archaeoctonus tuberculatus Pocock 1911, p. 19.
Archaeoctonus tuberculatus Petrunkevitch 1913, p. 34, and 1949, pp. 138–9, figs. 138, 176.
Alloscorpius tuberculatus Petrunkevitch 1953, p. 29, figs. 27, 28.

Material. Holotype, G.S.E. 9675 (or 456), 9676 (or 457). This specimen consists of part and counterpart preserved in grey shale with many plant remains. It was collected by James Bennie from the Coal Measures at Blair Point, near Dysart, Fife. Petrunkevitch (1953) states that it is now the only surviving specimen of several on which Peach (1881) founded his species *Eoscorpius tuberculatus*, making the assumption of specific identity between them, though some came from the Calciferous Sandstone of Lower Carboniferous age while this 'the first and best specimen' was from the Coal Measures. The two halves are not complete mirror-images of one another owing to thin slivers of shale having been lost. With the consent of Mr. R. B. Wilson I embedded both halves in Marco. This has made easily visible details that could not be seen before.

EXPLANATION OF PLATE 57

Figs. 1–3. *Benniescorpio tuberculatus* (Peach). 1, Carapace, G.S.E. 9676. ×6·75. 2, Ventral view of external impression of carapace, and dorsal view of the rest (cf. text-fig. 28). G.S.E. 9675. ×6·75. 3, Ventral view of supposed sternites XI, XII and bits of TXIII. G.S.E. 9676. ×6·75.

Remarks. When Peach described this specimen it was the first fossil scorpion to be found in Britain. Only four others were known—two from Europe (Corda 1835; 1839) and two from America (Meek and Worthen 1868). His reference of it to one of the American genera—*Eoscorpius*—must be read in this context. Since it is now clear that Peach's description is faulty in almost every detail (in part because it combines characteristics of 'scorpions' of vastly different ages), I name it *Benniescorpio* after its discoverer, James Bennie, who was a pioneer collector from the Scottish Carboniferous rocks (Bennie 1885). Since it possesses large lobed sternites I regard it as belonging to Pocock's group, Lobosterni.

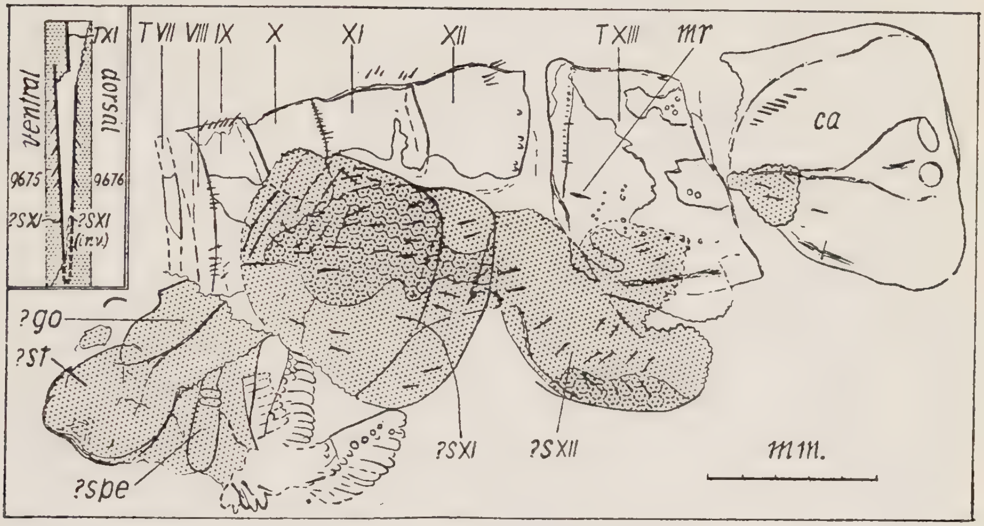
As pointed out by Peach, the carapace is upside down in relation to the body and lies near the tergal plate of segment XIII. This means that the dorsal aspect of the actual chitin of the carapace is seen on 9676, which elsewhere shows a ventral view of the ventral skin or of the internal cast of that skin where the chitin has been lost. On the other hand, 9675 displays the external cast of the carapace in ventral view, and at the same time the dorsal aspect of the chitin of the tergites and of the sternites (i.e. their inner surfaces), or of external casts of their outer surfaces (often with detached hairs adherent to the shale) where the chitin has been lost. There are also other complications resulting from folding and crumpling of the thin ventral skin and the displacement of the sclerites: in particular it seems necessary to postulate that one half of the supposed sternite XI has been folded dorsally on top of the other.

Diagnosis of genus and species. A rather large and relatively broad 'scorpion' with an almost square (8 mm.^{2}) carapace, having the general shape, position of median eyes, and ornament of *Lichnophthalmus pulcher* Petr.; no lateral eyes; the rest of the body about 20 mm. long, tergites only partly exposed but apparently normal in shape, non-tuberculate, but with lines of setae along the anterior borders and posterior margins of some of them; tergal plate XIII tuberculate with posterior margin abnormally broad; tail and sting unknown. Ventral organs somewhat displaced and obscure, but apparently an oval sternum and a large bilobed genital operculum; combs of pecten large, fin-like, with numerous teeth, and resembling those of *Lichnophthalmus pulcher*, Petr. Supposed sternite XI very long and broad, bilobed, coated with hairs. Supposed sternite XII also large and hairy, but its shape is unknown. Neither sternite has any stigmata.

Description. Dorsal organs

Carapace. This has been somewhat crushed, but the actual skin of its front part is wonderfully preserved in 9676, and part of the right side missing from 9676 can be restored from 9675 (Pl. 57, figs. 1, 2; text-fig. 29), but the hinder part has been lost. When complete it must have been nearly square in its crushed state. The present width in front is 8 mm. and its length is 7 mm., plus perhaps 2 mm. not preserved. The front margin is almost straight with a slight median projection (cf. *Lichnophthalmus*, Part 1, pl. 49, figs. 2, 3, 11, *ap*) and curves round in two semicircles at the sides. The carapace retains sufficient relief to show that it had a strongly elevated heart-shaped cephalic part with two anterior-lateral domes separated by a median furrow that divides in front into two grooves which almost encircle a prominent median eye-tubercle situated very near to the front of the shield. The tubercle carries two large, originally circular, eyes pointing upward and somewhat forward. The eye-tubercle and the two domes probably overhung

the anterior margin, as suggested by Peach, but the front corners of the carapace are perfectly exposed and exhibit nothing that can be taken for lateral eyes, which he states to be present. The external cast of the carapace on 9675 shows impressions of several parallel narrow ridges separated by fine linear markings. Though these lay on the external surface they may have been related to muscle attachments on the inside. They lie approximately on the posterior-lateral edge of the cephalic area. The postcephalic posterior-lateral corners of the shield are crumpled or missing everywhere, except for one doubtful fragment marked *?* on text-fig. 29 which can be seen on Pl. 57, fig. 1, to show a bit of a supposed lateral margin.



TEXT-FIG. 28. *Benniescorpio tuberculatus* (Peach). G.S.E. 9675, 9676. Holotype in dorsal aspect (except for the carapace), drawn in the same position as Peach's pl. 23, fig. 8, but with features that are only visible in 9676 restored to their true positions in relation to 9675: light stipple, ventral body plates with one layer of chitin preserved or as casts; dark stipple, ditto with two layers of chitin (one inverted); unstippled, dorsal plates, combs and external cast of carapace. Hairs (thick ends are proximal) represented here and there. *Inset*, diagram-section through Txi and ? Sxi as preserved in 9675 and 9676, i.e. the sternite in normal and inverted posture respectively (the outside being indicated by the hairs). *mr*, median ridge. For key to other abbreviations see p. 277.

Irregularly scattered small and large granules or tubercles are seen in several parts, the largest being concentrated on the sides of the median furrow. Their occurrence led Peach to bestow the specific name *tuberculatus* on this specimen. (However, he also described the tergites as covered with tubercles, which they are not; but he supported his view by pl. 23, fig. 8*f*, which refers to a specimen from the Calciferous Sandstone of Redhall.) The tuberculation recalls that on the carapace of *Lichnophthalmus pulcher* (Part 1, pp. 269, 271). Two long setae are seen attached, one to the eye-tubercle and one on the R. cephalic dome.

From the above description it will be seen that Petrunkevitch's ascription of the specimen to *Alloscorpius* and his 1953, fig. 27, are erroneous, the large postcephalic area which he shows being in reality part of tergal plate xiii.

Were it possible to identify a Carboniferous 'scorpion' by the carapace alone, this

creature could with assurance be designated *Lichnophthalmus pulcher* Petr., though in its crushed state the carapace gives the appearance of having been relatively narrower behind than in that species.

Tergites VII–XII. Parts of the six tergites are preserved in chitin and are exposed in dorsal view in 9675; and there are impressions on the 1st sternite of the linear margins of the other ends of TVII and TVIII, a fact which implies that they had been bent back dorsally and then squashed on to the sternite. Peach's description implies that the ends of the tergites are present, but none of the lateral margins that should define them is visible. What is exposed is the central sections of whole tergites which must have been much wider than the parts preserved suggest. TVII is very short—about 0·5 mm.; the next is *c.* 0·75 mm., and the rest increase in length gradually to TXII which is *c.* 3·25 mm. long. Though not always visible, there was certainly a linear anterior margin on each, and the posterior margin was an infold just in front of which in two cases (probably in all originally) is a row of setae, and on TVII and TXII a few isolated granules or mucrones. The rest of the tergite in each case is devoid of ornament, but there is evidence that it was hairy in places, long setae being preserved here and there. I have already mentioned that Peach's description of the tergites was not based upon this specimen and is quite inapplicable to it.

Tergal plate XIII. Parts of this are exposed on each of the pieces, but its outline cannot be seen. It appears to have been at least 5 mm. long, plus 0·75 mm., the length of the anterior border which carried a line of hairs. At right angles to this border near the point where the latter passes into folded skin is a short keel which may mark the mid-line. Small groups of largish tubercles seem to lie fairly symmetrically in relation to the mid-line suggested by the keel, but there are other granules whose distribution appears to be random. The posterior margin is indicated by a strong line. There is little to suggest that this plate had the marked tapering that normally characterizes TXIII, and it may be inferred from this that the tail was broader than usual.

Ventral organs

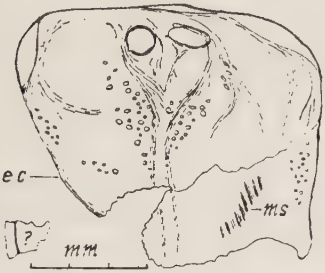
These were made of excessively thin skin, that of the sternites being coated with long slender hairs (Pl. 56, fig. 5) which pointed backwards, as in *Wattisonia*, above, p. 319. The skin has been crushed on itself, and crumpled or lost in places, while in others shale intervenes between the folds. This has resulted in the counterpart on 9676 not being everywhere the mirror-image of the fossil seen on 9675. I have attempted to incorporate in one text-fig. 28 details taken from both halves as they would appear in dorsal aspect on 9675 (cf. Peach's pl. 23, fig. 8). Some of the lines on the ventral skin seem to represent the impressions of dorsal features. For all these reasons the following description is tentative.

Supposed sternum of the prosoma (*st*), *genital operculum* (*go*), and *sternum of the pecten* (*spe.*). These lie at the left front of the specimen, but are very poorly preserved. The skin is devoid of the long hairs so conspicuous on the sternites (below). The sternum would seem to be an oval plate passing backwards into the two halves of the genital operculum, but the posterior part of the latter is not visible. Between these and the comb is a very obscure area that may represent the sternum of the pecten.

Peach may be referring to the above when he states on p. 399: 'Nothing can be said of the first two of the ventral plates, except that one of them bears the combs.'

The pecten. Both combs of the pecten lie folded on themselves and displaced to one

side of the body; but, as stated above, its sternum cannot be recognized with certainty. The specimen was the first Carboniferous 'scorpion' to display the detailed structure of the comb. Meek and Worthen (1868) say of the bit seen in *Eoscorpius carbonarius*: 'The single detached comb-like organ, seen lying in the matrix on the left side of the abdomen, shows some eleven or twelve of the little laminae or divisions, but apparently had more, as it is incomplete, at least at one end.' Peach (1881, p. 399) naturally described it fully and accurately as follows: 'They (the combs) seen to be made up of a broad triangular rachis ornamented with an irregular embossed scale-like pattern, which reminds one of that on *Eurypterus* and *Pterygotus*, and edged at the lower side with a row of comparatively large leaf-like teeth. These are constricted at their bases, they then suddenly expand, the sides then become parallel, and as suddenly become truncated to a blunt point. . . . In their present crushed state the individual leaflets overlap each other like the splints of a venetian blind.' The combs are therefore closely comparable with those of *Lichnophthalmus* (Part 1, p. 274). I would add that the bosses appear to be limited to that part of the rachis that adjoins the teeth, those nearest the latter constituting a row of fulcra which perhaps give the appearance responsible for the item 'constricted at their bases' in Peach's description. Some of the chitin, including several long hairs, is preserved in 9675. The piece of comb conspicuous in 9676 is unrecognizable in 9675.



TEXT-FIG. 29. *Benniescorpio tuberculatus* (Peach). G.S.E. 9675, 9676. Carapace, anterior part preserved in chitin on 9676; R. posterior-lateral part showing ? muscle scars (*ms*) restored from the external cast on 9675. *ec*, posterior-lateral edge of the inflated cephalic area; ?, doubtfully part of the carapace.

The *supposed sternite* XI lies to the right of the pecten (Pl. 56, fig. 5, Pl. 57, figs. 2, 3; text-fig. 28). Of this Peach says: 'The third is an apron-like flap, narrow in front and widening posteriorly, and rounded at the angles. It is as deep as three of the dorsal plates, opposite which it is placed. Within the postero-lateral angles of this plate two fine slits occur which are the openings into the air sacs.' This last statement is not true; perhaps he was misled into regarding hairs or a narrow seam of chitin as openings (stigmata). I think Peach was also mistaken in other respects. Examination of both halves and of the now transparent chitin forces me to regard his 'apron-like flap' as a bilobed sternite with its two lobes symmetrically folded on to one another so that the two lateral margins lie almost exactly superimposed where they adjoin the tergites, and the two posterior margins likewise lie one almost above the other behind, while the common mid-line forms the edge now adjacent to the combs. Further, about one-fifth of the length of the sternite in front of its hind margin is another line, perhaps marking the extent of overlap of SXI on to SXII. Where the skin is doubled, both this line and the linear posterior margin are duplicated. The parts where the double structure is preserved in chitin has a dark stipple on text-fig. 28. As I interpret it, this area represents the remnants of the L. lobe lying turned over dorsally and seen in dorsal view in 9675. Most, if not all, of the R. lobe is exposed in ventral view in 9676, and it is this skin which is seen in 9675 to pass under one of the tergites (see section in text-fig. 28). I can detect no pleural skin connecting sternites to tergites, as described by Peach, p. 399: 'longitudinally folded thinner skin which is constricted opposite the articulations'.

At the front end of Sxi are a number of lines, one of which may be its anterior linear margin. The others are in my opinion the impressions of the margins of two or possibly three of the anterior tergites turned over and twisted diagonally backwards.

If the above interpretation be correct, the sternite was not only abnormally long (as pointed out by Peach), but also abnormally wide. The large size of the sternites is a noticeable feature in other Lobostern 'scorpions'.

Remains of a second large sternal plate, clearly displayed on both specimens (Pl. 57, figs. 2, 3), and here regarded as Sxii, lies behind the one I have just described, but the directions in which the hairs on it point suggest that it has been displaced and twisted round through about 120°. On one side the skin has also been bent on itself so that the hairs on it point in the opposite direction to those on the main sheet. The original outline of the sternite can nowhere be seen, but it must have been comparable in size with Sxi.

One area of chitin which lies ventrally below Txiii, and another scrap which is below the inverted carapace, both have hairs pointing posteriorly. It may be part of the same sclerite.

It is a pity that so little can be deduced with certainty about the original shape and organization of this animal, individual parts of which show so much. The carapace agrees closely with that of *Lichnophthalmus pulcher* Petr., but there is no proof, only a strong presumption that it belongs to the associated body. The pecten also matches well that of *Lichnophthalmus*, and one sternite at least is bilobed; the sternites, however, have the long hairs of *Wattisonia*, whereas *Lichnophthalmus* showed only minute spinules, and those sited on the doublure.

The above description shows that the sternites of this creature in no way resemble those of any Orthostern 'scorpion'; and therefore it must be excluded from the Eoscorpionidae (*Auct.*). On the other hand, it is almost certainly an aquatic Lobostern with unique characteristics meriting its own generic name.

CONCLUSIONS

A. Anatomical. 1. The carapace, including its eyes, the dorsal plates of the body, the caudal rings, and the poison-capsule and sting of the Carboniferous 'scorpions' here studied differ in no essential feature from the homologous parts of Recent scorpions which lack lateral eyes (I can, however, confirm Petrunkevitch's statement that there are Carboniferous forms with lateral eyes; e.g. *Compsoscorpius elongatus* Petr. and *C. elegans* Petr.).

2. Our knowledge of the ventral anatomy is much less complete; but in all the forms here examined there is also an essential similarity between the macro- and microscopic structure of the following organs and the homologous parts of present-day scorpions. In the prosoma—the chelicerae, pedipalps, mouth parts, and legs (though the latter may differ in detail); in the mesosoma—the sense-organs on the pecten.

3. The 'scorpions' here described fall into two groups when the shape, structure, and probable functions of the sternites and pectines are considered.

Group A. Sternites strongly overlapping, each larger than its corresponding tergite, and resembling a pair of the laminate, gill-bearing appendages of an Eurypterid. The combs large, fin-shaped, and with many teeth.

(i) Sternites strongly bilobed and with spinules on the doublures:

(*a*) Coxa 3 with epicoxite, abuts against an hexagonal sternum; coxa 4 abuts against the genital

operculum which is bilobed as in Recent scorpions. At least one leg ends in denticulate claws with 'stiletto heels'. Sternites with hairy coating on external surface. *Pareobuthus salopiensis*

(*b*) Chelicerae abnormally large, sternum unknown, coxa 4 does not abut against the genital operculum which has a median ridge flanked by paired, two-bossed lateral wings; legs with denticulate claws with 'stiletto heels'; some tarsal spurs replaced by leaf-like structures; no hairs observed on external surface of the sternites. *Lichnophthalmus pulcher*

(ii) Sternites unlobed, some with a median suture; hairs on their external surfaces and on the doublures. Chelicerae abnormally large; coxae 1, 2 with mandibular processes and the whole coxo-sternal area as in Recent scorpions; genital operculum as in (i) (*b*); distribution and shape of spurs and claws as in Recent Buthids, but all claws and some spurs are denticulate. *Mazoniscorpio mazonensis*

Group B. Sternites slightly overlapping and not much larger than corresponding tergites, resembling those of Recent scorpions but with no stigmata on their external surface. Stigmata not yet observed with certainty, but possibly present on the posterior-lateral doublures. The combs not fully known, but probably with narrower rachis and fewer teeth than in Group A, and therefore more similar to those of Recent scorpions.

This group cannot yet be subdivided. Its members have the following additional characteristics: Coxo-sternal area and the genital operculum essentially the same as in Recent scorpions. The shape and distribution of spurs and claws on the legs and the shapes and proportions of the chelicerae and pedipalps, and the distribution of granules, setae, and trichobotheria on them can be closely matched in present-day Buthid scorpions; but the claws and some of the spurs are denticulate in all the larger specimens. *Buthiscorpius buthiformis*, *B. major*
and probably G.S.M. Za 2924, Za 2925 and M.M. L8194.

There is not enough of *Benniescorpio tuberculatus* or *Wattisonia coseleyensis* preserved to allow them to be placed with certainty, but I consider that the former may belong to Group A(i)(*a*) and the latter to some part of Group A.

I have also examined the holotype of *Archaeoctonus glaber* Peach (G.S.E. 9675, 9676). Judged by its sternites and the little that can be seen of its pecten, it would fall in Group B; but the abnormal structure of its coxo-sternal region and the remarkable shortness of its legs, both features being regarded by Pocock as diagnostic characteristics of his genus *Archaeoctonus*, cannot be matched in any of the specimens here described. On the other hand, the claws, so far as they can be examined (the specimen is adherent to shale), appear to resemble all the larger claws described above in being denticulate (though denticles are only obscurely visible on one leg) and in possessing (at any rate on the 4th leg) a large dagger-type pad (figured by Peach on pl. 22, fig. 2*h*) recalling that on the supposed 3rd leg of *Lichnophthalmus* (Part 1, text-fig. 7).

B. Ecological. In drawing inferences from the anatomy as to the mode of life and habitat of Carboniferous 'scorpions' it must be remembered that the homologous organs in Recent forms, however similar in structure they may be—and this dearth of change since Palaeozoic times is one of the most awkward facts facing an evolutionist—have all been inherited from their Carboniferous ancestors, and not vice versa. Can it be assumed that these unchanged organs have today the same functions as they had in Carboniferous times, or is it possible that there has been an adaptation of the functions to new environments without any modification of the shape and structure of the organs?

An example of this problem is found in the uniformity of structure (though not always in shape) of the pecten with its sensory hairs on the rachis and its sensory fields of peg-organs on the teeth, whether the comb belongs to a Recent terrestrial scorpion, to a supposedly terrestrial Carboniferous or Triassic 'scorpion', or to an almost cer-

tainly aquatic one like *Lichnophthalmus* (or for that matter the certainly aquatic ? Merostome '*Glyptoscorpius*').

Another example is the sting which is an organ that at first sight would appear to be adapted exclusively to a terrestrial way of life, but which is known to have been developed in at least two purely aquatic Merostomes, *Carcinosoma scorpionis* Grote and Pitt (late Silurian) and *Mixopterus kiaeri* Størmer (? early Devonian).

With such reservations in mind, the following inferences suggest themselves: (i) From anatomical conclusions 1 and 2, above, it is arguable that the mode of locomotion, perception of light by the eyes, and of other vibrations by the peg-organs of the pecten, by setae and by trichobothria and the methods of hunting, capture, and stinging of their exclusively animal food, practised by those Carboniferous 'scorpions' here described, were the same as those employed by Recent scorpions, despite the fact that most of the latter live in tropical dry regions, under stones or buried in sand (to retain their internal moisture), whereas their Coal Measures ancestors, whether aquatic or terrestrial, were denizens of swamps and rain-forests of an equatorial belt.

(ii) Ecological analysis of anatomical conclusion 3 and of the grouping there set out is more complex.

(*a*) The structure of the pecten, the sternites, and the tarsalia of the legs (particularly the claws and spurs) of animals in Group A(i) (*a*) (*b*), and of the pecten and sternite in Group A(ii) appear to be better adapted for an aquatic than for a terrestrial life; yet the tarsalia of *Mazoniscorpio* (Group A(ii)) so closely resemble their Recent homologues (in the Buthidae) that this creature must have been capable of walking on land. However, there would seem to be room for gills above the laminate sternites of all the forms in Group A and in *Benniescorpio*; and there is visual proof that there were no stigmata on the sternites of any of the specimens examined. I infer that all the animals in Group A were gill-breathers, and that they were, nevertheless, capable, like *Limulus*, of spending part of their life on land. It is noteworthy that in two specimens in Group A in which the genital operculum is known, it is different in shape from and more complex than that organ in 'scorpions' of Group B where it closely resembles the operculum of Recent forms. There is nothing to indicate whether this difference can be correlated with a difference in habitat or in reproductive processes (in a third specimen in Group A, *Pareobuthus*, the genital operculum is simply bilobed as in Recent forms).

(*b*) I am inclined to infer that all the 'scorpions' in Group B were terrestrial, since every part of the exoskeleton, barring the sternites, has been handed down to the scorpions of today virtually unmodified, there having been no adaptations needed to fit the animal for its present exclusively terrestrial habitat, except perhaps the development of true air-breathing book-lungs above the sternites. It may ultimately turn out that even this type of respiration had already been acquired by the 'scorpions' in Group B; yet undoubted stigmatic openings for such book-lungs have not so far been observed either on the external surface of the sternites, as in Recent forms, or on their doublures, as in Triassic ones, or on any other part of the body. Nor does there seem enough overlap of the sternites to have housed gills. The only other method of respiration that suggests itself to me is by direct oxidation of the blood through the skin, which in several cases has been seen to be penetrated by numerous pore-canals, and which in every case is extremely thin on the ventral surface. It must be recalled that in Triassic and Recent scorpions respiration takes place through a film of chitin that covers the laminae of the

lung-books. In the Carboniferous 'scorpions' of Group B such oxidation may perhaps have been particularly effective in the small infolds of the skin created by the overlap of the sternites (i.e. in the same positions as the gills of Group A), which were kept perpetually moist by the water-laden atmosphere of the coal-swamps. This could have been a first step towards the development of true book-lungs which by Triassic times had come into existence above the sternites, but which had stigmata on the posterior-lateral doublures, that is, in the same positions as the gill-pouches of *Lichnophthalmus* and *Mazoniscorpio*, and not, as today, on the external surface of the sternites.

In appraising the validity of the hypothesis of respiration through the thin ventral skin it should be borne in mind that experiments on Recent scorpions have shown that 'they have considerable respiratory reserves' (Cloudley-Thompson 1958, p. 74)—in other words a scorpion can survive for long periods under conditions in which there is a deficiency of air; e.g. at the bottom of deep burrows that have collapsed or with seven out of its eight lungs blocked.

To summarize the foregoing conclusions in a general statement I advance the following tentative opinions:

1. There were two races of 'scorpions' living side by side in the very humid surroundings of the Carboniferous coal-swamps. One race, mostly but not entirely, with lobate sternites were aquatic animals breathing by gills in gill-pouches lying above deeply overlapping sternites, and possessing large fin-like combs. Some of these were adapted to crawl easily over weeds, others had normal scorpion legs. Probably all were capable of living out of water for fairly long periods. The second race were terrestrial creatures, with short orthostern sternites, breathing air in some way at present unknown, but possibly by book-lungs housed above the sternites with openings into modifications of the gill-pouches seen in the other race. *Mazoniscorpio* seems to possess some characteristics of each race, having the large combs and deeply overlapping sternites of the first, yet with all its other organs fashioned exactly as their homologues in the second race.
2. Both races had many organs fashioned like their homologous parts in Recent Buthid scorpions, but it was from the second that the Buthidae have descended. (It is interesting in this connexion to find that the Buthidae have a more primitive type of embryonic development than the Scorpionidae, see below; and that those genera that have metatarsal spurs also have pentagonal sternums as in the Carboniferous 'scorpions' here described.)
3. Judging from published information, there were Carboniferous 'scorpions' whose ventral structures (particularly the coxo-sternal parts) differed greatly from those discovered by my research. Development of such 'scorpions' by the present technique might show how far these differences really exist and how far each specimen is unique or referable to either of the two races, postulated above.
4. What has been learnt from this research does nothing towards solving the impasse in which palaeontologists find themselves, in the matter of classification of the Carboniferous 'scorpions', as a result of imperfection of preservation and rarity of specimens (see also Part 1, p. 267). This impasse is hardly to be wondered at when we consider that zoologists with complete specimens of hundreds of species from half a dozen continents at their disposal have been forced to employ an admittedly artificial classification

of Recent scorpions. This classification takes into account such things as the shape of the pincers and the sternum, the number of trichobothria on the pincers and of spurs on the legs, while placing within a single Order creatures whose embryological developments may be radically different. 'We see that although so much alike in outward appearance, there exist great internal differences between various scorpions. In some as in the Buthidae the embryo is left to feed itself on the yolk of the egg, while in others, as in the Scorpionidae, embryonic nourishment is a complex affair resulting from a process of mutual adaptation between the organs of mother and young' (M. Vachon, *Endeavour*, April 1953, p. 89). Existing palaeontological classifications have made an analogous mistake in assuming that all Carboniferous 'scorpions' were terrestrial air-breathers, though Pocock, when instituting his Group Lobosterni, expressed more than a suspicion that 'respiratory lamellae' lay above the lobes of the sternites.

ADDENDA

1. *An error in my description of* Lichnophthalmus pulcher *Petr.* In the light of discoveries in *Mazoniscorpio*, my preferred interpretation of the sternum of the pecten of *Lichnophthalmus pulcher* Petr. in Part 1 (p. 272 and text-fig. 4) is clearly erroneous; for what I tentatively interpreted as anterior plates of a complex sternum of the pecten (text-fig. 4*a*, *b*, *p*, *p′*) can be matched closely with the genital operculum of *Mazoniscorpio* (present text-fig. 12), and the posterior plates with the whole sternum of the pecten in the latter.

The discovery of the shape and structure of the genital operculum and sternum of the pecten in *Mazoniscorpio* also throws doubt on Pocock's interpretation of these parts in *Eobuthus holti* Pocock (1911, pl. 11, fig. 2 and text-fig. 1).

2. *The pecten of scorpions and* 'Glyptoscorpius'. In Part 1, p. 263, I stated that the pecten is an organ only found in scorpions, whether fossil or living, provided we except the 'doubtfully Eurypterid *Glyptoscorpius*', and that I had made preparations of the teeth of a *Glyptoscorpius* 'comb' and had found 'them to be devoid of the peg-organs so characteristic of the scorpion comb, whether fossil or Recent'. This statement remains true for the specimen B.M. In.25982 that I examined which is undoubtedly conspecific with *G. caledonicus* Salter, as figured by Peach (1882, pl. 29, figs. 17, 17*a–d*), agreeing, as it does, in size and in having barb-like spines along the two sides of the teeth or filaments. In all my preparations the skin is quite structureless (Pl. 53, fig. 5). However, I have now found that a very similar comb (B.M. In.42706) attributed in the British Museum catalogue to *Glyptoscorpius*, which differs from *G. caledonicus* Salter in that the teeth or filaments have no spines along their sides, differs also in possessing typical peg-organs rather widely scattered over its surface (Pl. 53, fig. 6).

Both these combs are parts of gigantic Arthropods, of a size met with in some Merostomata, but monstrous when compared with the largest-known scorpion. The teeth (filaments of Peach) of the first specimen (In.25982) range up to about 12 mm. in length, and those on the second comb (In.42706) up to 6 or 7 mm.: yet the peg-organs on the latter are about the same size as those on the tiny *Buthiscorpius buthiformis* (Pl. 46, fig. 5) and on that of the medium-sized *Lichnophthalmus pulcher* (Part 1, pl. 50, figs. 2, 3) and the unnamed G.S.M. Za 2925 (Pl. 55, fig. 4), in all of which they are closely packed together. I wish to thank Dr. Waterston and Dr. E. I. White for allowing me to examine these important specimens of what is certainly a geological enigma.

3. *Improvement in technique.* Since writing Part 1, I have made a great improvement in the technique described on p. 264. Instead of inverting the specimen after etching in order to get rid of the debris and isolated pieces of the skin, I now suck up the acid with a pipette until the specimen is nearly dry, lift it out of the evaporating basin and, inclining it slightly over a white basin full of water, I wash it with a very gentle stream of water from a pipette. This carries the remaining acid, the mud, and any loosened bits of chitin into the basin, from which the chitin can be extracted with a brush or pipette as described in Part 1; but as a rule most parts of the skin remain attached to the body. When the washing is finished, the specimen is put on the microscope stage and flooded gently for inspection, &c., before the next etch. As soon as the 'well' in the Marco has been established round the fossil, the washing should aim at moving the mud into one corner of the 'well', but even this operation should be

carried on over a white basin in case any chitin fragments get washed over the sides. The mud and fragments are then sucked up from the corner by pipette and ejected into water in a white basin.

In dealing with the larger specimens, I have found that it is possible to etch the appendages free from the matrix, and yet retain them attached to the body or to the Marco-cast right up to the end. As is shown by Pl. 50, fig. 2 and Pl. 51, fig. 4, such isolated parts of the body can eventually be dried and then flooded with Marco, there to remain floating in their natural postures within the final Marco-block.

When the fossil has been embedded in the Marco-block, details cannot be so easily seen as when the individual organs have been extracted and mounted. For this reason in one or two cases I intentionally broke away particular organs with a needle during the etching, and mounted them on slips, after having previously recorded their position on the animal by a photo (Pl. 50, fig. 2; Pl. 51, figs. 4, 6). The chief value of this modification of the original technique lies in the opportunity it gives to see the organs in their original positions before they may become detached, accidentally or intentionally.

4. *Extraction of chitin from shale.* In dealing with the chitinous skin of 'scorpions' *preserved in shale*, I have found that a covering of Marco, ground level and sealed with glass, increases greatly the contrast between chitin and shale and at the same time gives a transparency to the chitin that it does not possess when 'dry' (see the photos of *Benniescorpio*, Pl. 56, fig. 5; Pl. 57). In one case after the specimen had been covered with Marco the underlying shale on the reverse was wetted and dried several times and finally all of it was picked off with a needle, leaving the chitin beautifully transparent and attached to the Marco. The great objection to this treatment is that the Marco cannot be removed after it has polymerized.

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PROFESSOR L. J. WILLS
Farley Cottage,
Romsley,
near Birmingham

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THE PELTASPERMACEAE, A PTERIDOSPERM FAMILY OF PERMIAN AND TRIASSIC AGE

by JOHN A. TOWNROW

ABSTRACT. The three genera comprising the Peltaspermaceae, *Lepidopteris* (leaf), *Antevsia* (pollen organ), *Peltaspermum* (seed organ) are discussed. The following are redescribed: *L. stormbergensis* (Seward) Townrow, *L. martinsii* (Kurtze) comb. nov., *A. zeilleri* (Nathorst) Harris, *A. extans* (Frenguelli) comb. nov., and *P. thomasi* Harris. The evidence for referring isolated organs to their parent plant, and the morphology and affinities of the family are considered. The Peltaspermaceae range from the Thuringian to the Rhaetic (inclusive), the earliest species coming from Europe.

THE Peltaspermaceae were established by Dr. H. Hamshaw Thomas as a small family of Triassic (including Rhaetic) age. They have now been found in the Upper Permian, but only once from rocks later than the Rhaetic. The leaves, *Lepidopteris*, have been known for many years. The pollen organ, *Antevsia*, has hitherto been known from one species; herein a second is described. The seed organ, *Peltaspermum*, is known from two species, but only the type species, *P. rotula*, in detail.

The Rhaetic *P. rotula* is peltate and radially symmetrical, and is thus unique among seed organs. This has led to the belief that the Peltaspermaceae are very isolated morphologically. Examination of the earlier species suggests that the family is not so isolated, and that comparison is possible with Carboniferous fossils.

The ages and distribution of the species of the Peltaspermaceae are shown in Table 1.

LEPIDOPTERIS Schimper

Type species *L. stuttgardiensis* (Jaeger) Schimper 1869

The genus *Lepidopteris* has been redefined and discussed by Frenguelli (1943) and Townrow (1956). Of the five leaves referred to *Lepidopteris*, the youngest, *L. ottonis* (see Antevs 1914; Harris 1932; Lundblad 1950), and the two oldest, *L. stormbergensis* (see Thomas 1933; Townrow 1956) and *L. martinsii* (see below), are known in detail; but the other two, *L. stuttgardiensis* and *L. madagascariensis*, are very incompletely known (Townrow 1956). The finding of thirty-five new specimens of *L. stormbergensis* has added new information on the range of variation of that species, and on the morphology of *Lepidopteris*. This latter with characters of the rachis is taken in the general discussion of *Lepidopteris*; they both are of wider interest, and support the reference of reproductive organs to the leaves.

The gross form of the leaf. In *L. stormbergensis* the pinnae are offset towards the upper (adaxial) side of the rachis, for on this side they are traceable almost to the mid-line of the rachis; but upon the lower (abaxial) side are overlapped by the rachis. Which side is the upper or lower is determined by reference to the leaf base. *L. martinsii* is probably the same as *L. stormbergensis*; the main rachis forms a trench whose bottom lies at a deeper level than the bottom of the trenches formed by the pinna rachises (text-figs. 1A–D, 4A). The matter has not been discussed in the other species.

[Palaeontology, Vol. 3, Part 3, 1960, pp. 333–61, pl. 58.]

The pinnules of *L. stormbergensis*, and probably of the other species, are set obliquely on their rachises, so that if the pinna is considered to be inclined the pinnules lie horizontally (text-fig. 5A, B, E, H; and see Schimper 1869, pl. 34, fig. 1; Harris 1932, pl. 6, fig. 2 and pl. 8, figs. 15, 16). Both asymmetry of pinna insertion and an oblique pinnule insertion seems to be common, if not normal, in living and fossil pinnate leaves.

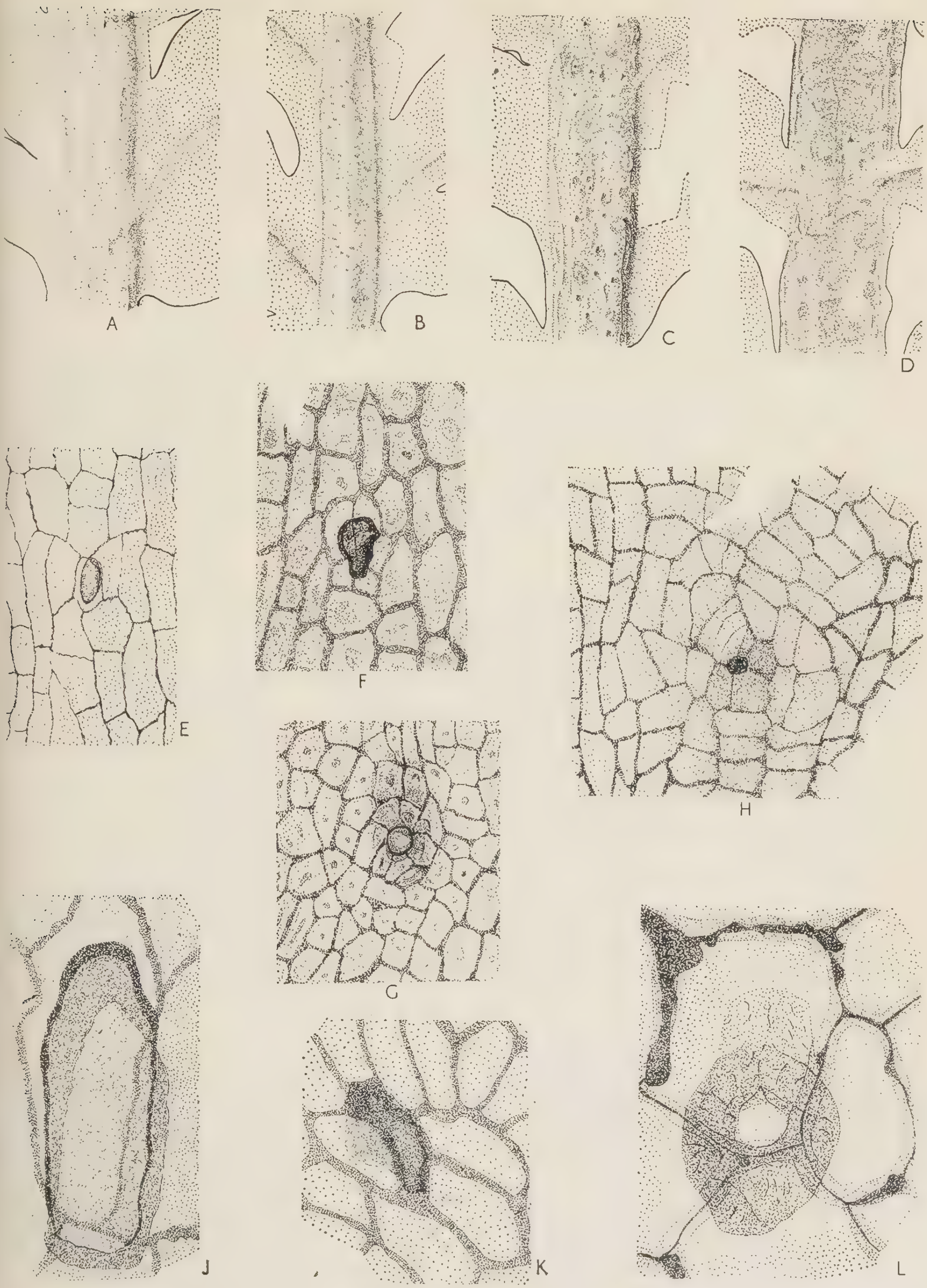
TABLE 1

The Peltaspermaceae

Organ	*Species*	*Geological horizon and age*	*Distribution*
Leaf	*Lepidopteris martinsii*	Kupferschiefer, Obere Zechstein, Marl Slate, Hilton Plant Bed, Lower Marls and Limestone; Upper Permian	Germany, England
Leaf	*Lepidopteris stormbergensis*	Uppermost Beaufort, Molteno, Esk Series, Hawkesbury Sandstone, Estratos de Potrerillos, ? Sakanema; uppermost Lower and Middle Trias	South Africa, Queensland, New South Wales, the Argentine (? Madagascar)
Pollen organ	*Antevsia extans*	Uppermost Beaufort, Molteno, Estratos de Potrerillos; uppermost Lower and Middle Trias	South Africa, the Argentine
Seed organ	*Peltaspermum thomasi*	Molteno; Middle Trias	South Africa
Leaf	*Lepidopteris stuttgardiensis*	Schillfsandstein; Lower Keuper	S.-W. Germany (? Urals)
Leaf	*Lepidopteris madagascariensis*	Sakanema; Middle and ? Upper Trias	Madagascar
Leaf	*Lepidopteris ottonis*	Rhaetic zone fossil	Sweden, Germany, E. Greenland, China, Kazaghistan (? Tonkin)
Pollen organ	*Antevsia zeilleri*	Scoresby Sound Beds, Scanian Coal Measures; Rhaetic	Sweden, E. Greenland
Seed organ	*Peltaspermum rotula*		

In all species of *Lepidopteris* zwischerfiedern occur. These are pinnules set directly on the rachis between adjacent pinnae. In *L. martinsii* some of these pinnules lie on the abaxial rachis surface, appearing to be in series with the pinnules on the pinnae (text-fig. 5J). In four specimens of *L. stormbergensis* the lowest pinnule of a pinna is orientated differently from its neighbours, and is set partly on the abaxial rachis surface (text-fig. 4G). In two of these specimens there are also pinnule tufts, or their remains, inserted

TEXT-FIG. 1. A–J, *Lepidopteris stormbergensis*. A–D, Series of rachises showing increasing degree of lumpiness; A, C, D, adaxial surface exposed, B, abaxial surface exposed; ×7·2. E–H, Rachis cuticles from specimens figs. A–D, showing increasing proliferation at trichome bases; ×200. J, Trichome set on a single cell, top somewhat torn; ×876. K, *L. ottonis*, trichome set on a single cell; ×392. L, *L. martinsii*, trichome set on a single cell, and showing vertical extensions of cell outlines; the pale area in the centre of the trichome is probably a feebly cutinized part of trichome base; ×879 (V/5793).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purely on the abaxial rachis surface, but lying in series with the pinnae (text-fig. 4H). In the other specimens the zwischerfiedern are lateral, joined to one another by a wing of tissue with lamina-like cuticle, but the lowest zwischerfiedern are inserted nearer the abaxial rachis surface than the pinnae. In *L. ottonis* and *L. stuttgardiensis* no difference in level between the pinnae and zwischerfiedern is apparent in published figures.

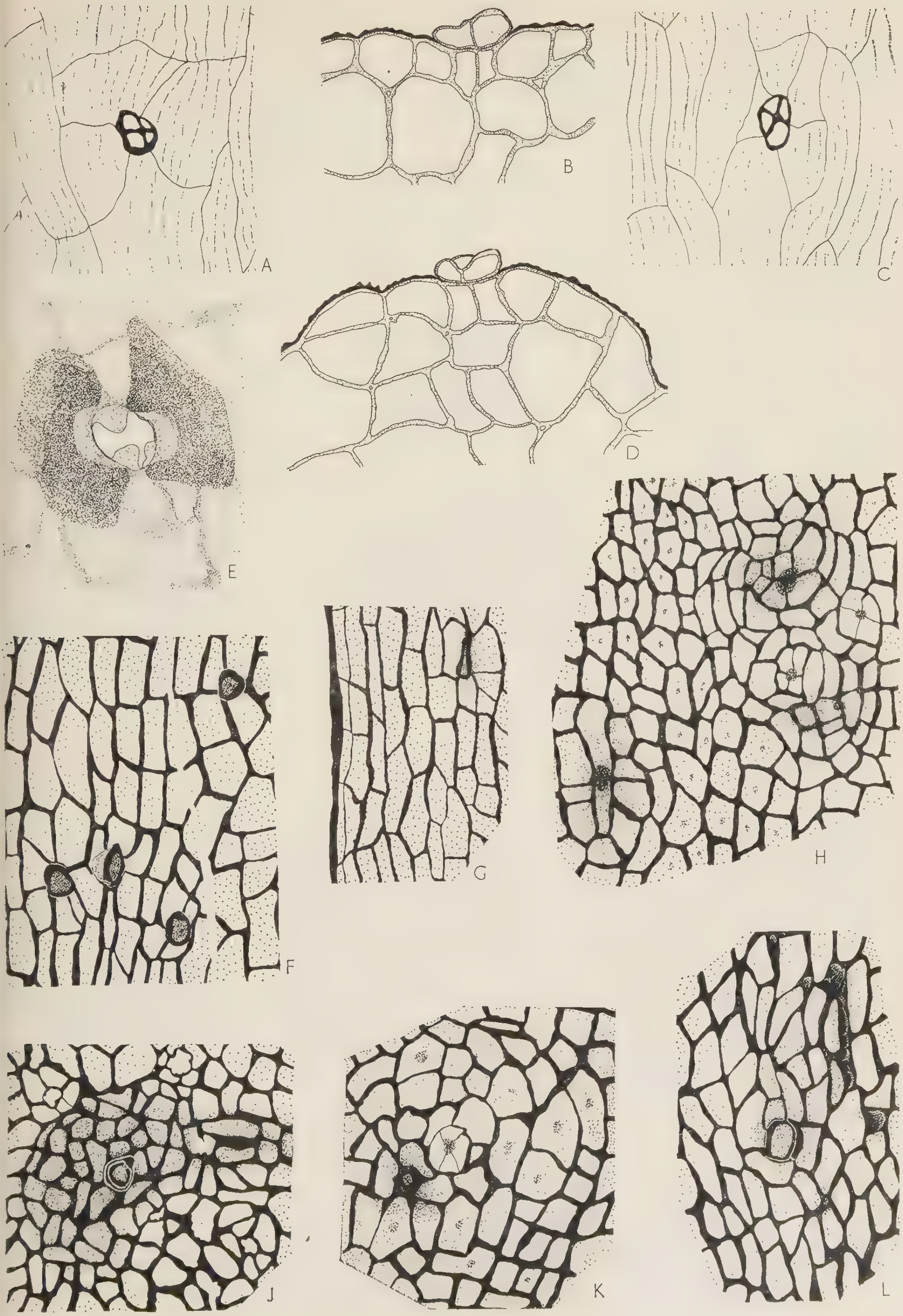
I suggest that this series may be interpreted as a progressive simplification of the leaf. In *L. martinsii* the series of pinnules normally continues, as zwischerfiedern, on to the abaxial rachis surface; in *L. ottonis* and *L. stuttgardiensis* it is wholly lateral and at one level, while *L. stormbergensis* is intermediate.

The leaf-base and vascular trace. Five leaves of *L. stormbergensis* showed the bulbous leaf-base (text-figs. 4E, F; 5C, D, H). It is cutinized on one side only (the abaxial) and here there are strong wrinklings suggesting the compression of a terete organ, and blisters are missing. The cell rows run laterally (text-fig. 4C). On the adaxial surface short cells, without any pattern, are visible, and also two bulges which recall the vascular trace scars on an abscission surface, and from each bulge an indistinct rib can be traced upwards. These ribs join about 1 cm. from the leaf-base; the one rib can then be traced the whole length of the leaf (text-fig. 4F). The ribs are wholly internal, giving dark matter on incomplete maceration, but leaving no mark on the cuticle. I suggest they represent the remains of vascular tissue. There is no information about the vascular trace from the other species.

The structure of the rachis. The swellings on the rachis of *Lepidopteris* were first regarded as scales, but were later shown to be blisters of the cuticle (Antevs 1914). In *L. stormbergensis* there is a series of leaves from some with a smooth rachis to others with a markedly blistered one. From this series one can suggest the nature and origin of the blisters.

On leaves with a smooth rachis, the rachis cuticle shows trichomes, or trichome bases (often numerous), either set on a single cell, or with slight proliferation of the epidermal cells around the trichome base (text-figs. 1A, B, E, F; 2E), the other cells lying in longitudinal rows. On leaves with a slightly blistered rachis the proliferation around the trichome bases is greater (text-figs. 1C, D, G, H; 2F), the area of proliferation corresponding to a small blister. In leaves with a markedly blistered rachis the proliferation is greater still, either to give an area up to twenty cells across in which the cells are set in a concentric pattern (text-fig. 6F), or, rarely, the compressed blisters overlap and the cells appear to be set irregularly. Sometimes, over large blisters, a trichome base is not visible, but usually some trace of it remains. More than one trichome may contribute to a single blister (cf. text-fig. 6F).

TEXT-FIG. 2. A–D, *Rumex hydrolapathum*. A, Trichome on a smooth petiole (cuticle prep.). B, Section of outer tissues of a smooth petiole passing through a trichome. C, Trichome over a swelling, showing slight proliferation of cells (cuticle prep.). D, Section of a swelling beneath a trichome; A–D ×326. E–K, *Lepidopteris stormbergensis*. E, A naturally macerated stoma, showing arcs of dark matter (probably lignine lamellae) flanking stomatal pit; ×730. F, Cuticle of a smooth rachis, showing one trichome and trichome bases. G, Rachis cuticle showing one trichome base, and cell outlines over wing (to left). H, Cuticle of a slightly lumpy rachis, showing trichome bases, proliferated cells, and two stomata. K, Stem cuticle, showing stoma, trichome base over a proliferation. J, *L. martinsii*. Rachis cuticle, trichome base over a proliferation and four stomata (left plain) (V/5963 a). L, *L. ottonis*. Rachis cuticle showing a trichome base and slight proliferation. E–L all ×167.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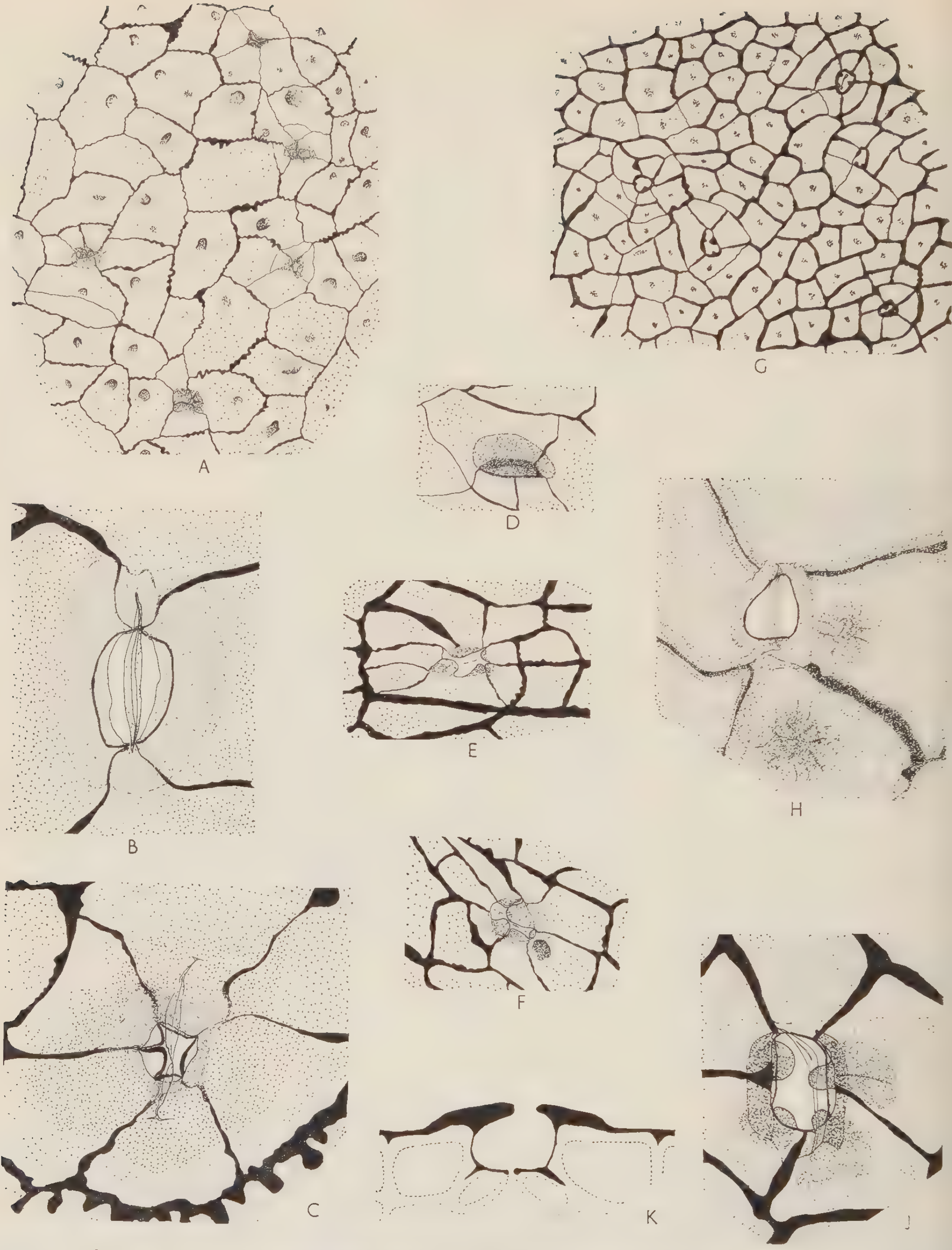
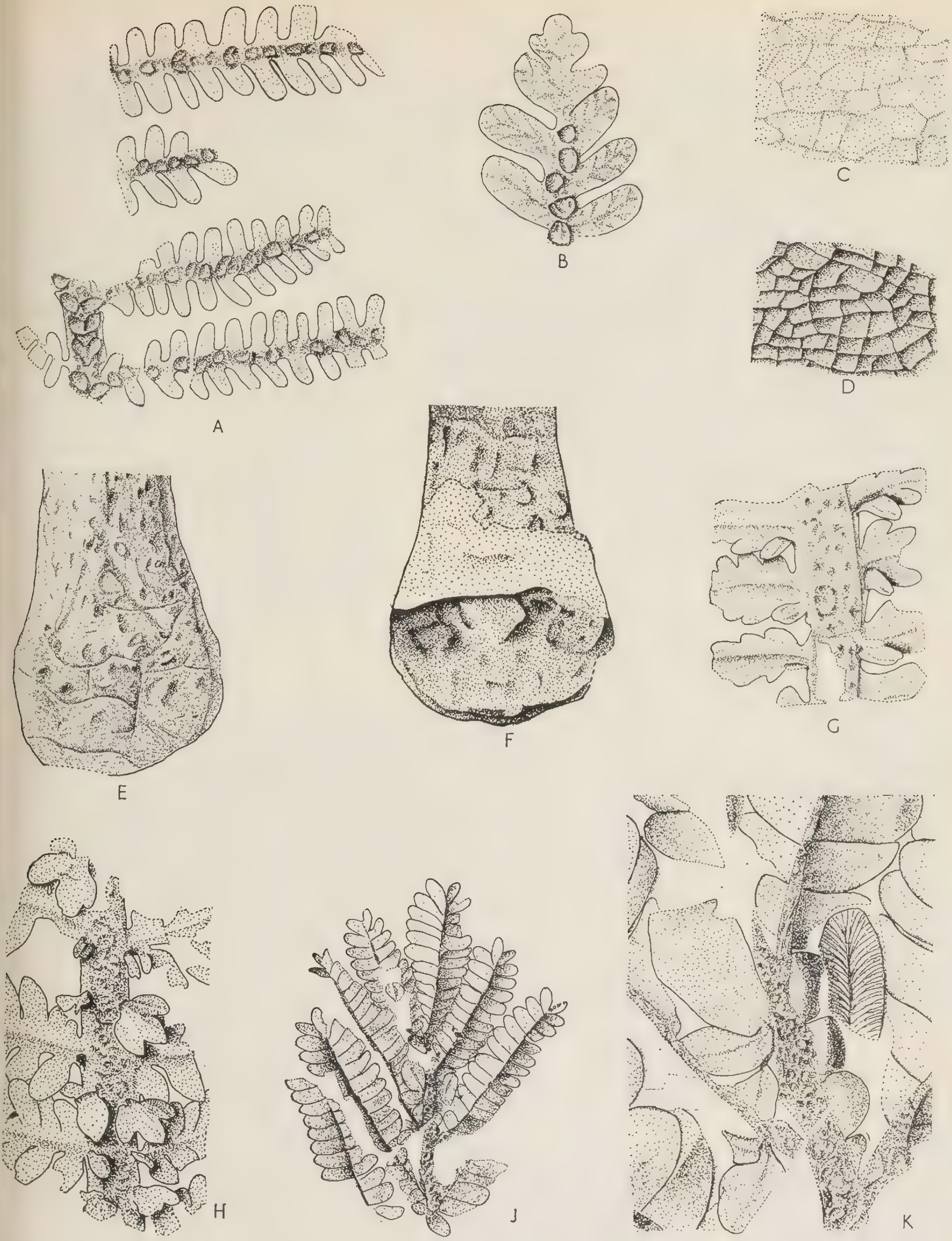


TEXT-FIG. 3. A–C, *Lepidopteris stormbergensis*. A, Cuticle from lamina showing cell outlines, papillae, and stomata; ×167. B, Stoma without cutin papillae; ×876. C. Stoma of normal form; ×876. D–E, *Antevsia extans*. Trichome from the rachis; ×392. E, Stoma from the rachis; ×392. F, *Peltaspermum thomasi*. Stoma from the rachis; ×392 (V/23400). G–K, *L. martinsii*. G, Cuticle from lamina showing cell outlines, papillae, and stomata; ×167 (V/5963 b). H, Stoma lacking cutin lappetts; ×876 (the Hellstedt leaf). J, Stoma with large lappets of solid cutin; ×876 (V/5963 b). K, Section, approximately transverse, reconstructed through stoma shown at J; ×876 approx.



TEXT-FIG. 4. A–B, *Lepidopteris martinsii*. A, Part of a leaf showing decurrent pinnules and more or less paired imprints of swellings on rachises; ×1·6 (v/5963). B, A pinna apex, showing venation and imprints of swellings; ×2 (v/2595). C–H, *L. stormbergensis*. C, D, Cells from abaxial (C) and adaxial (D) surfaces of leaf base; ×106. E, F, Surfaces of the leaf base (E abaxial, F adaxial), showing suggested vascular traces; ×7·2. G, Part of a leaf, showing insertion of lowest pinnule of pinnae partly on abaxial rachis surface; ×7·2. H, Leaf, showing pinnule tufts set on the abaxial rachis surface; ×1·7. J, K, *Paripteris gigantea*. J, Leaf, abaxial side; ×0·4. K, Central part of same leaf showing blisters on rachises, two pinnule tufts on abaxial rachis surface (to left) and venation in one pinnule; ×1·6 (v/1296).

Rumex hydrolapathum [Polygonaceae] provides an analogy. In this plant the petiole bears trichomes, and in some leaves the trichomes are set on small swellings, which show, in a cuticle preparation, proliferated epidermal cells around the trichome base, and in section proliferation of the sub-epidermal layer, which raises the swelling (text-fig. 2A–D). Presumably, therefore, the swellings of *L. stormbergensis* are also formed by sub-epidermal proliferation at the site of a trichome; and the proliferation of the epidermis takes place to accommodate this local increase in girth. In *Lepidopteris*, however, the blisters contain a dense coaly residue, soluble on maceration, suggesting that the blisters were occupied by thick-walled lignified cells rather than cellulose parenchyma.

L. ottonis and *L. martinsii* show the same features as *L. stormbergensis* (text-figs. 1K, L; 2J, L), except that in *L. ottonis* solitary trichomes and small blisters are only seen at the leaf or pinna apices, and blisters lacking any sign of a trichome are commoner (Antevs 1914, pl. 2, figs. 6–8). Further, the reproductive structures show, as far as is known, blisters on their rachises just like those of *L. stormbergensis*, though usually smaller.

The trichomes appear to be unicellular, more or less spherical (text-fig. 1J, K, L), and are very thinly cutinized, the cuticle being minutely functate.

The stomata. One or two naturally macerated leaf fragments with stomata were found. These stomata showed two arcs of dark matter flanking the stomatal pit, and lying on the guard cell surface (text-fig. 2E). These are interpreted as lignine lamellae upon the outward surface of the guard cell, seen generally in living gymnosperms.

The stem of the Lepidopteris *plant.* Text-fig. 5C shows what is possibly the stem of *L. stormbergensis*. Both ends are broken, and at present it measures 2·3 cm. long an 0·5 cm. wide. The surface is of low relief, but shows a number of more or less contiguou raised areas. The cuticle (text-fig. 2K) is as on the rachises. The stem is wider than an rachis seen, and differs further in lacking a wing (Townrow 1956; and text-fig. 2G).

This stem closely resembles the stem referred to *L. ottonis* (see Harris 1932), though i is smaller and with a more delicate cuticle. Since both stems are cutinized they are presumably primary organs. There is no information as to how the leaves were borne.

Lepidopteris stormbergensis (Seward) Townrow

Plate 58, fig. 1; text-figs. 1A–H, J; 2E–H, K; 3A–C; 4C–H; 5A–H; 6A–C; 8H

For synonomy and diagnosis see Townrow 1956

Description and discussion. Nearly all the material of *L. stormbergensis* comes from the

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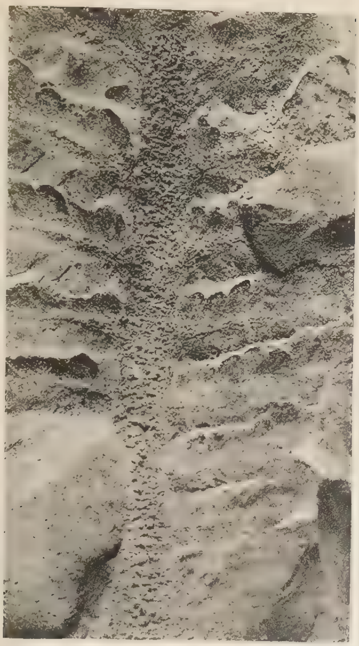
EXPLANATION OF PLATE 58

Fig. 1. *Lepidopteris stormbergensis* (Seward) Townrow. Leaf with abnormally lumpy rachis, ×1.

Figs. 2, 3. *Peltaspermum thomasi* Harris, v/23400, Brit. Mus. (Nat. Hist.) Part and counterpart of type, ×2.

Figs. 4–9. *Antevsia extans* (Frenguelli) comb. nov. 4, 5, Pollen grains, sulcus facing observer (4) and to left (5), ×500. 6, The type (from du Toit 1927, pl. 29, fig. 3), × 1·7. Specimen showing branching, ×1. 8, 9, Upper and lower surfaces of disk and pollen sacs (different specimens), ×3. (*st*—branchlet, or position of same.)

Fig. 10. *Antevsia zeilleri* (Nathorst) Harris. Pollen grains in three views, ×500.



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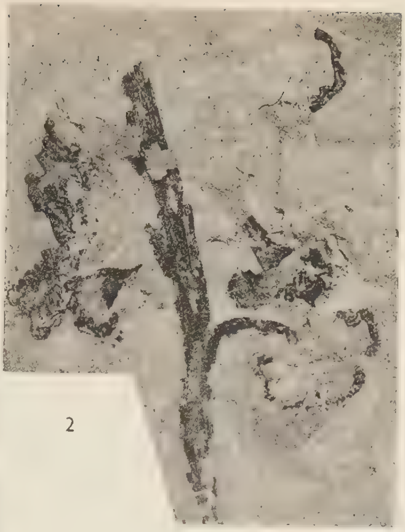

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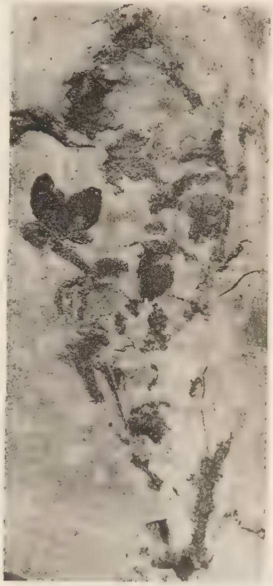

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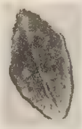

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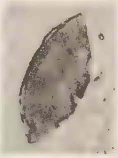

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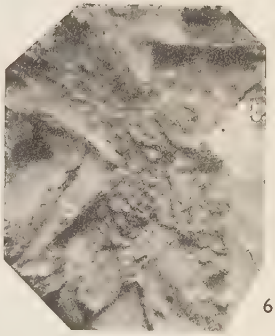

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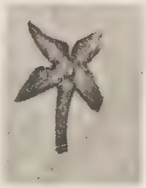

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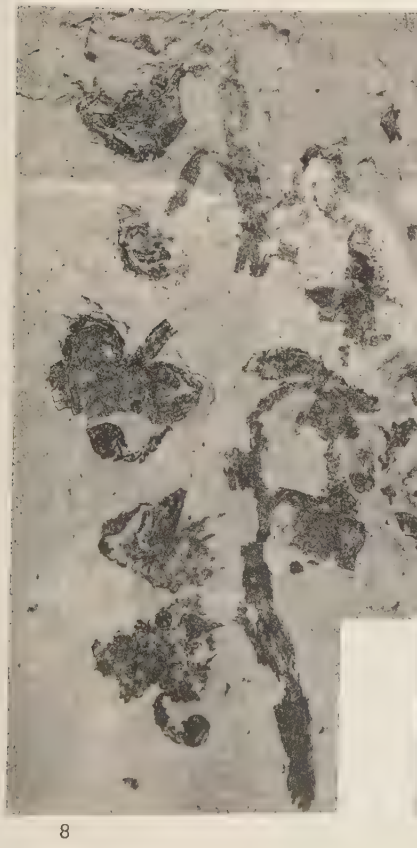

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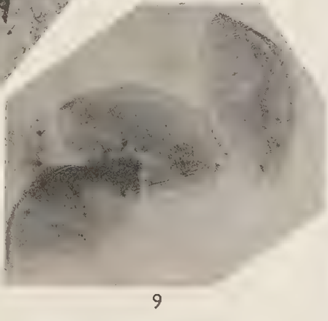

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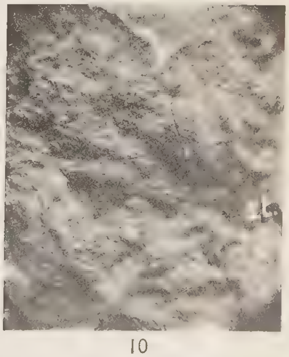


10

Burnera Waterfall locality, Upper Umkomaas, Natal; but two leaves are from the Australian Trias (v/32106 and v/32472, Brit. Mus. (Nat. Hist.)). The Waterfall locality is regarded as falling within the Middle Triassic Molteno (see Haughton 1954; Townrow 1957). At the Waterfall the leaves of *L. stormbergensis* are found scattered more or less evenly through the thickness of plant-bearing rock; and this is different from the other common leaves, which are markedly patchy.

L. stormbergensis proves to be a variable leaf, and the variation is set out in Table 2 and in text-figs. 3A–C; 5A–H; 6A–C.

TABLE 2

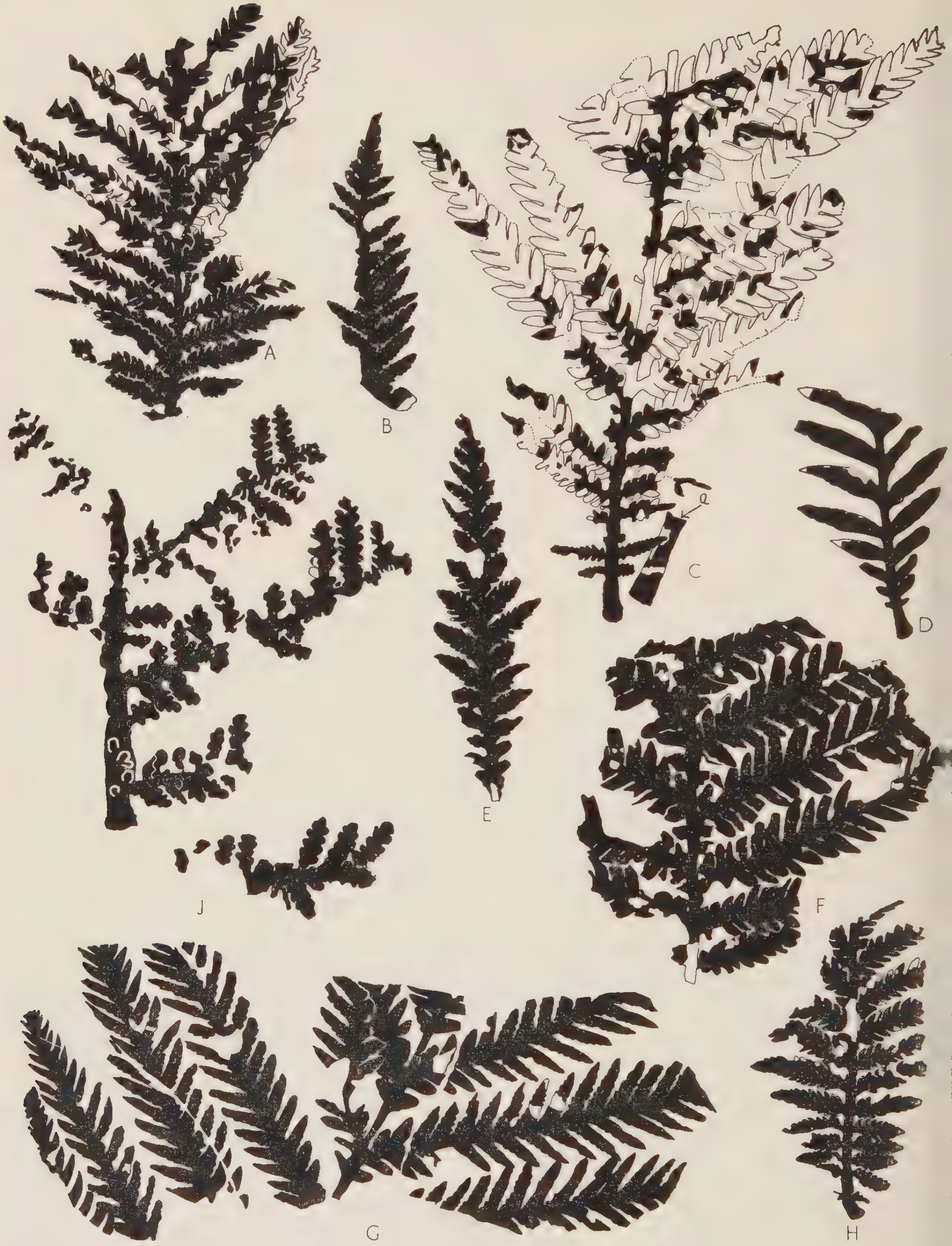
Range of variation in *L. stormbergensis*

Variation	*Characters showing variation*				
	Leaf length	*Leaf width*	*Pinna length*	*Pinnule length*	*Pinnule width*
Largest	20 cm.	13 cm.	7 cm.	14 mm.	7 mm.
Normal	12 cm.	8 cm.	4 cm.	6 mm.	4 mm.
Smallest	7 cm.	2·5 cm.	1·3 cm.	3 mm.	2 mm.
	Cell size (away from veins)	*Size of sinuosities of cell outlines*	*Height and width of papillae*	*Cuticle thickness*	
				Upper	*Lower*
Largest	60 μ	5 μ	4 μ, 10 μ	3·5 μ	3·0 μ
Normal	45 μ	2–3 μ	1 μ, 5 μ	2·0 μ	1·0 μ
Smallest	24 μ	0·5 μ	0 0	1·5 μ	0·5 μ
	Number of subsidiary cells	*Stomatal frequency mm.^{2}*	*Stomatal index*		
Most	8	108	9·3		
Normal	5 or 6	34	7·0		
Least	3	20	4·7		

The stomata are all of essentially the same pattern, but they differ in detail. The commonest sort (about 75 per cent.) shows subsidiary cells bearing a cutinized papilla, now hollow (text-fig. 3C). A second sort, making up nearly all the remainder, shows a lappett of solid cutin (cf. text-fig. 3J). One or two leaves showed some stomata of an abnormal sort (text-fig. 3B). These stomata (about 1 per cent.) are important, for they match a sort of stoma seen on the pollen sacs of the pollen organ referred to *L. stormbergensis*.

Though variable, I do not believe that species other than *L. stormbergensis* are present. The groups given in Table 3 intergrade, and no other character gives ground for splitting up the material. The characters vary about one mean, and if more than one species was involved this would scarcely be so. Such characters are the number of pinnae per leaf (about 32), the interval between veins (about 0·25 mm.), the stomatal density and index, and the stomatal form.

A list of records believed to be synonyms of *L. stormbergensis* is given by Townrow (1956); in only one of them was the cuticle examined (Thomas 1933). The variation in



TEXT-FIG. 5. A–H, *Lepidopteris stormbergensis*. Leaves to show variation in gross form, stem shown in C at *a*; ×0·75 (G is V/32472). J, *L. martinsii*. Large tripinnate leaf, showing pinnules on abaxial surface, and zwischerfiedern between pinnae; ×0·75 (redrawn from Gothan and Nagalhardt 1921, pl. 3, fig. 1).

gross form of the present material easily includes the variation seen in these records, and the cuticle of Dr. Thomas's specimen is typical.

I have examined two Australian specimens of *L. stormbergensis* (v/32106 and v/32472, Brit. Mus. (Nat. Hist.)) and Mr. J. M. Pulley has very kindly sent me some excellent photographs of other leaves from Queensland (described but not figured by Walkom 1924 and 1929), which, though only one has a cuticle, with nearly straight cell outlines, I identify as *L. stormbergensis*. These photographs show the same variation as the Natal leaves. I think that there is no doubt that the same leaf is involved in both Australia and South Africa.

TABLE 3

Variation in a number of characters in *Lepidopteris stormbergensis*

	Specimen	*Leaf length/ width*	*Lumpiness of rachis*	*Cuticle thickness (μ)*		*Stomatal density (per H.P. field)*		*Stomatal index*		*Averages*
				Upper	*Lower*	*Upper*	*Lower*	*Upper*	*Lower*	
GROUP I	1	3·6	A							*Stomatal density*
	8	..	A	3·5	3·0	3·0	1·4	10·4	5·6	
	18	3·6	B	2·0	1·0	2·8	1·2	9·6	5·0	upper 2·6
	11	..	A	3·0	1·5	2·2	1·0	7·3	4·3	lower 1·5
	16	..	B	2·0	1·0	1·6	1·2	5·3	4·1	both 2·0
	A	2·7	C	3·5	3·0	3·0	1·4	10·5	5·6	
	10	1·5	B	2·0	0·5	2·8	1·0	8·4	5·2	*Stomatal index*
	9	..	A	2·0	1·0	2·2	1·4	7·1	4·9	upper 8·7
	12^{+}	1·7	D	3·0	1·0	2·6	1·4	6·6	3·9	lower 5·1
	23^{+}	..	D	2·0	0·5	4·2	3·0	10·0	7·6	
	15^{+}	2·3	B	2·0	2·0	1·4	1·2	5·5	4·6	both 6·9
GROUP II	7	1·7	D	3·0	2·5	2·4	2·6	7·6	9·3	*Stomatal density*
	6°	..	E	2·0	1·5	1·8	2·8	7·3	9·9	
	34	..	C	2·0	1·5	1·4	1·6	5·0	5·2	upper 1·48
	33	1·5	D	2·0	1·5	1·0	1·2	5·0	6·6	lower 2·4
	22	..	C	2·0	1·5	1·4	2·0	5·6	7·2	both 1·96
	27^{+}	..	E	1·5	1·0	2·0	3·0	6·6	9·6	
	4	1·3	E	3·5	0·5	1·8	2·6	6·5	8·4	*Stomatal index*
	5°	..	D	3·5	0·5	2·2	3·0	7·5	9·4	upper 6·25
	B	..	B	2·5	0·5	0·2	2·2	0·8	9·3	lower 8·45
	30°	..	E	3·0	2·0	2·4	3·4	7·6	11·0	
	31^{+}	..	D	2·5	1·5	2·8	1·8	9·0	6·6	both 7·35

Notes: (i) Rachis quantities A–E refer to 5-figd. rachises (text-fig. 1A–D; pl. 58, fig. 1) taken as standards. (ii) Leaves marked $^{+}$ exceptional in one value. (iii) Leaves marked °, the length/width probably less than 1·5, but specimen too small for certainty. (iv) Counts averages of $10\frac{1}{6}$ in. fields.

The possible habit of L. stormbergensis. The leaves of *L. stormbergensis* can be placed in two groups. In the first the leaves are narrow, with smooth or nearly smooth rachises, and with more stomata on the upper (adaxial) leaf surface than on the under (abaxial) surface. In the second group the leaves are wide, the rachises blistered, and the distribution of stomata normal (Table 3).

In many, but by no means all, waterside herbs of the British flora the leaves arising from the upper and lower nodes are of different form. The difference parallels the variation between the two groups found in *L. stormbergensis* (see Table 4 for some examples). Also, to refer again to *Rumex hydrolapathum*, the swellings on the petiole

TABLE 4

Stomatal densities (per H.P. field) and indices of some waterside herbs

		Upper surface		*Lower surface*		*Upper surface*		*Lower surface*	
Species	*Leaf position (mode)*	*Stomatal density*	*Stomatal index*	*Stomatal density*	*Stomatal index*	*Stomata counted*	*Cells counted*	*Stomata counted*	*Cells counted*
Alisma plantago	Upper	2·8	9·1	2·0	7·5	21	211	21	257
	Lower	3·5	4·6	1·8	8·0	35	266	22	254
Menianthes trifoliata	Upper	1·8	4·75	3·66	8·7	22	441	44	461
	Lower	4·0	6·8	4·7	7·0	39	533	47	630
Mentha aquatica[1]	Upper	0	0	12·2	17·2	0	317	72	346
	Lower	2·8	11·0	4·7	13·0	28	230	47	317
Myosotis palustris[2]	Upper	6·5	12·0	13·6	27·0	65	477	136	365
	Lower	6·8	15·0	6·1	14·0	68	392	61	377
Nasturtium officinale	Upper	8·1	20·0	11·6	27·0	81	398	116	308
	Lower	9·3	25·0	5·7	16·5	93	271	57	292
Polygonum amphibium	Upper	0·9	2·7	5·0	17·3	9	325	50	245
	Lower	13·8	22·0	7·0	18·0	138	489	69	317
P. hydropiper[1]	Upper	0·9	2·5	18·0	22·0	9	355	85	331
	Lower	4·0	13·2	5·0	13·2	35	231	41	269
Ranunculus flamula	Upper	6·0	18·0	3·7	16·5	71	323	44	226
	Lower	7·8	20·0	1·25	5·5	78	306	15	264
Rumex hydrolapathum	Upper	2·3	9·2	3·0	12·0	28	270	36	230
	Lower	4·8	14·5	4·4	10·5	48	282	44	376
Sium angustifolium	Upper	2·9	7·1	15·7	26·0	29	382	157	543
	Lower	4·7	11·7	4·2	9·6	47	352	42	397
Typha latifolia[3]	Upper	21·5	20·0	24·0	22·0	129	501	145	528
	Lower	22·0	24·0	16·0	27·0	65	477	136	365
Veronica beckabunga	Upper	8·0	16·0	14·5	25·0	80	422	145	437
	Lower	7·6	22·0	5·5	17·0	89	317	66	321

[1] Hair bases not counted. [2] On side shoots. [3] In stomatiferous areas only.

are characteristic of leaves from the upper nodes; the leaves from the lower nodes are smooth.

In Dicotyledonous trees stomata are generally few or absent on the leaf upper surface. In terrestrial Dicotyledenous herbs stomata may be frequent on the upper leaf surface, but they are regularly still more abundant on the under leaf surface, whatever the position of the leaf on the plant (see Salisbury 1927; Walter 1951). There are exceptions to this statement, but among plants which have more protected upper leaf surfaces as the Graminae, *Trifolium* (see Erban 1916), or cushion-forming alpines (see Salisbury 1927).

In these respects *L. stormbergensis* is more like a waterside herb than a tree or terrestrial herb. It might be argued that its rather thick cuticle is against this, but in fully adult leaves of *Rumex hydrolapathum* or *Alisma plantago* the cuticle, as prepared by oxidative maceration, may be up to 2·5 μ thick.

Lepidopteris martinsii (Kurtze) comb. nov.

Text-figs. 1L; 2J; 3G–K; 4A, B; 5J; 6D

1839 *Alethopterin martinsii* Germar MS; Kurtze, p. 34, pl. 3, fig. 2. German material, type specimen.

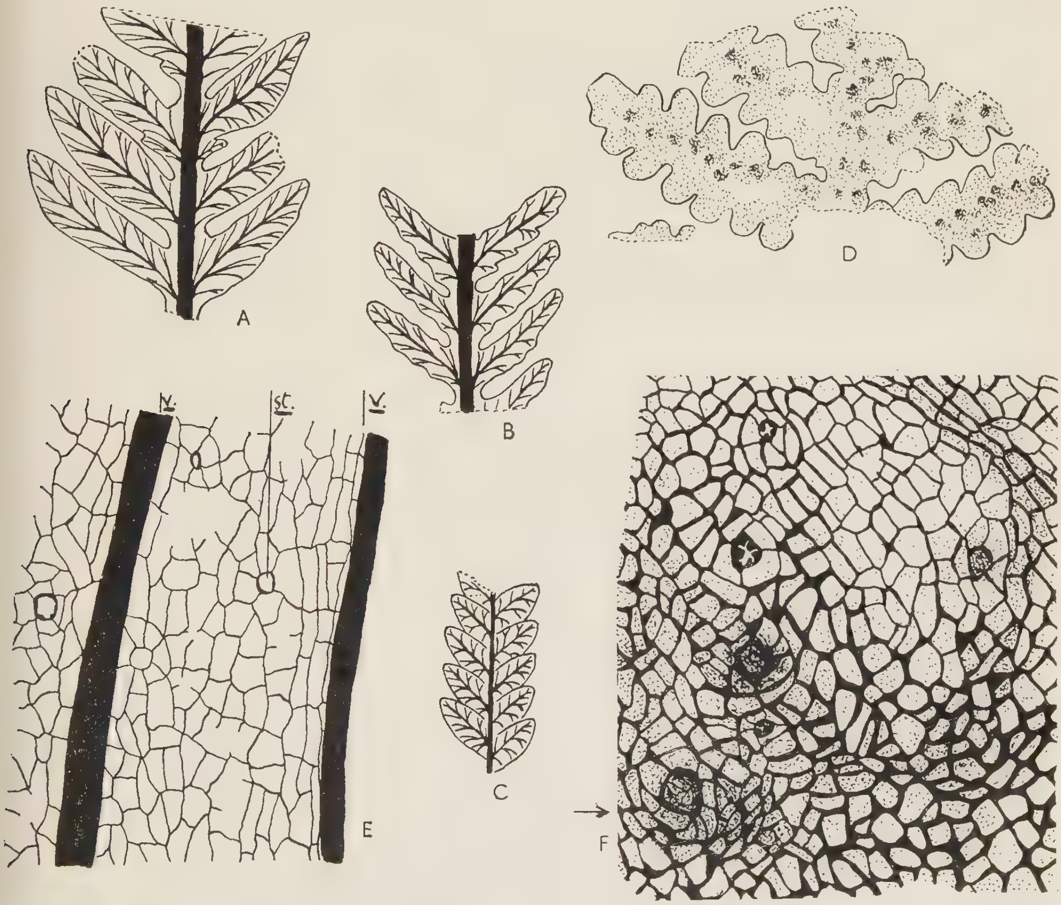
1907 *Callipteris martinsii* (Germar); Gothan, pp. 1–4, figs. 1, 2. German material figured.

1921 *Callipteris martinsii* (Germar); Gothan and Nagalhardt, pp. 451–3, pl. 6, figs. 5, 6; pl. 7, figs. 1–3. Good German material with cuticle.

1958 *Callipteris martinsii* (Germar); Stonely, pp. 313–15, pl. 37, figs. 2, 5; text-figs. 5, 6. English material, cuticle figures.

(For full synonomy see Gothan 1907 and Stoneley 1958.)

Diagnosis (emended). Leaf bipinnate, sometimes tripinnate, pinnules parallel-sided with very obtuse apex. Zwischerfiedern simple or pinnate, in smallest leaves absent, forming



TEXT-FIG. 6. A–C, *Lepidopteris stormbergensis.* Pinnules to show venation; ×1·33 (B is V/32472). D, *L. martinsii.* The Hellstedt leaf, showing form and swellings; ×1. E, *Paripteris gigantea.* Portion of naturally macerated cuticle, showing cell outlines, veins (*v*) and supposed stomata (*st*); ×53 (V/1293). F, *L. ottonis.* Cuticle over a large swelling, showing three trichome bases each over a proliferated area of cells, somewhat concentric cell arrangement at swelling margins, and two stomata; ×66.

a series from pinna base towards abaxial leaf surface. Blisters prominent. Cell outlines usually straight, sometimes showing minute processes running horizontally, but regularly with peg or strap-shaped processes at the cell corners running vertically. Stomatal pit usually overhung by small lappetts of solid cutin borne partly on the anticlinal surface of the subsidiary cells. Encircling cells often absent.

Description. The material described comes mostly from the Marl Slate of Kimberley (Notts.), with some from the Hilton Plant Bed (Westmorland). These horizons are approximately equivalent to the Kupferschiefer (Stoneley 1958). One additional leaf from the Zechstein of Hellstedt (referred to as the Hellstedt leaf) was most kindly lent me by the Director, Paleobotaniska Avdelningen, Naturhistoriska Riksmuseet, Stockholm. The English material is all in the collections of the British Museum (Nat. Hist.). It is rather fragmentary, few specimens have a cuticle, and only the Hellstedt leaf is cutinized over the main rachis.

The leaf is shown in text-figs. 4A; 5J. The larger specimens figured in the literature are tripinnate, and the smaller bipinnate. In some German specimens the series of zwischerfiedern can be seen continuing on to the abaxial rachis surface, but in my specimens the lowest pinnule of a pinna is simply somewhat decurrent (see, for example, Gothan and Nagalhardt 1921 and text-figs. 4A; 5J). The rachises of all the specimens show rather prominent swellings, or imprints which are interpreted as them remains; frequently rather regularly in pairs (text-figs. 4A; 6E). On the cuticle trichomes and trichome bases surrounded by proliferated cells can be seen (text-figs. 1L; 2J). The venation is shown in text-fig. 4B; the distance between the veins at the margin is about 0·75 mm.

The features of the cuticle are shown in text-figs. 2J; 3G. On both lamina and rachis one cuticle is thicker than the other. I suppose that the thinner cuticle is from the lower surface of the leaf. The cell outlines in two of the English specimens (V/5963b and V/5964) show in places minute processes, less than 1 μ high (text-fig. 3G). In all the specimens, especially over the rachis, the cutin on the periclinal cell walls penetrates rather deeply, sometimes lying crushed on one side, sometimes still upright so that the various levels can be determined by focusing. All also show projections of cutin inwards at least at the cell corners, up to 3 μ long (text-figs. 1L; 3H). In V/5963 the cells also show each a single (often obscure) papilla set more or less centrally; all the other leaves have a smooth cuticle.

The stomatal density is about 40 mm.^{2} (upper surface) and 80 mm.^{2} (lower surface); and the stomatal index about 7 (upper surface) and 14 (lower surface) (count of 20 high-power fields). About three-quarters of the stomata examined showed lappetts of solid cutin overhanging the stomatal pit, and in about a tenth of these lappetts were so large as almost to close the stomatal pit, but normally were much smaller (text-fig. 3G, J). The stomata without lappetts showed a rim of thick cutin (text-fig. 3H). The lappetts were set partly on the anticlinal surface of the subsidiary cells, so that they pointed obliquely upwards, and did not lie in the same plane as the cuticle surface (text-fig. 3J, K).

Various thin places and irregular holes, presumably pathological, and smaller holes and irregularities that were probably caused by sand damage (the holes were about the same size as the grains of the matrix) were present.

Discussion. Many specimens of *L. martinsii* have been figured, and these form an intergrading series; most fall between the extremes, and the series is not easily divisible into more than one entity. The cuticle has been much less studied (see Gothan and Nagalhardt 1921; Florin 1931; Stoneley 1958), but here too there seems to be a gradation of forms that cannot conveniently be divided. Not enough cutinized specimens have been examined, however, to say whether there is any correlation between leaves of a certain form and certain cuticle characters. Stoneley (1958) points out that in the German specimens whose cuticle has hitherto been figured the cuticle is papillate, whereas in the English specimens the cuticle appeared to be smooth. However, staining in safranin shows that in at least one English leaf there are papillae, and in at least one German leaf there are not.

The similarity between *L. martinsii* and species of *Lepidopteris* has been noted before (e.g. by Gothan 1907), and *L. martinsii* is now removed from *Callipteris*, and placed in *Lepidopteris*, because it agrees in the construction of the leaf, particularly in its series of zwischerfiedern; in the detailed construction of the blisters on the rachis; and in overall stomatal construction, which is of a rather unusual sort. This extends the range of the genus *Lepidopteris*, and therefore of the Peltaspermaceae, from the Thuringian to the Rhaetic.

L. martinsii may be distinguished from *L. ottonis* and *L. stormbergensis* by its parallel-sided and obtuse pinnules, by the details of its stomata (text-figs. 5J; 3J) and by the presence of cutin projections inwards at the cell corners. A tripinnate specimen may be told from the bipinnate *L. stuttgardiensis*, but a smaller specimen may look like *L. stuttgardiensis*. They may then be distinguished because *L. stuttgardiensis* has, it appears, shorter pinnules.

ANTEVSIA Harris 1937

Type species *Antevsia zeilleri* (Nathorst) Harris

Diagnosis (emended). Microsporophyll bipinnate, primary branching alternate, in one plane, second branching irregular. Main and branch rachises with blister-like swellings. Ultimate branches bearing four to twelve pollen sacs. Pollen sacs sessile, unilocular, 2–5 mm. long and 1–2 mm. wide, dehiscing by a longitudinal slit on ventral face. Pollen-sac wall massive, showing midrib and a few stomata on dorsal surface. Interior cuticle lining pollen sac absent, all other parts cutinized, and showing stomata overhung by hollow or solid cutin papillae. Pollen grains oval with slight projection at each end, monosulcate, sulcus same length as grain, lips of sulcus touching or almost touching along its whole length. Cuticle without other markings. Length 23–40 μ, width 13–28 μ, depth 12–25 μ, ratio length/width about 1·7.

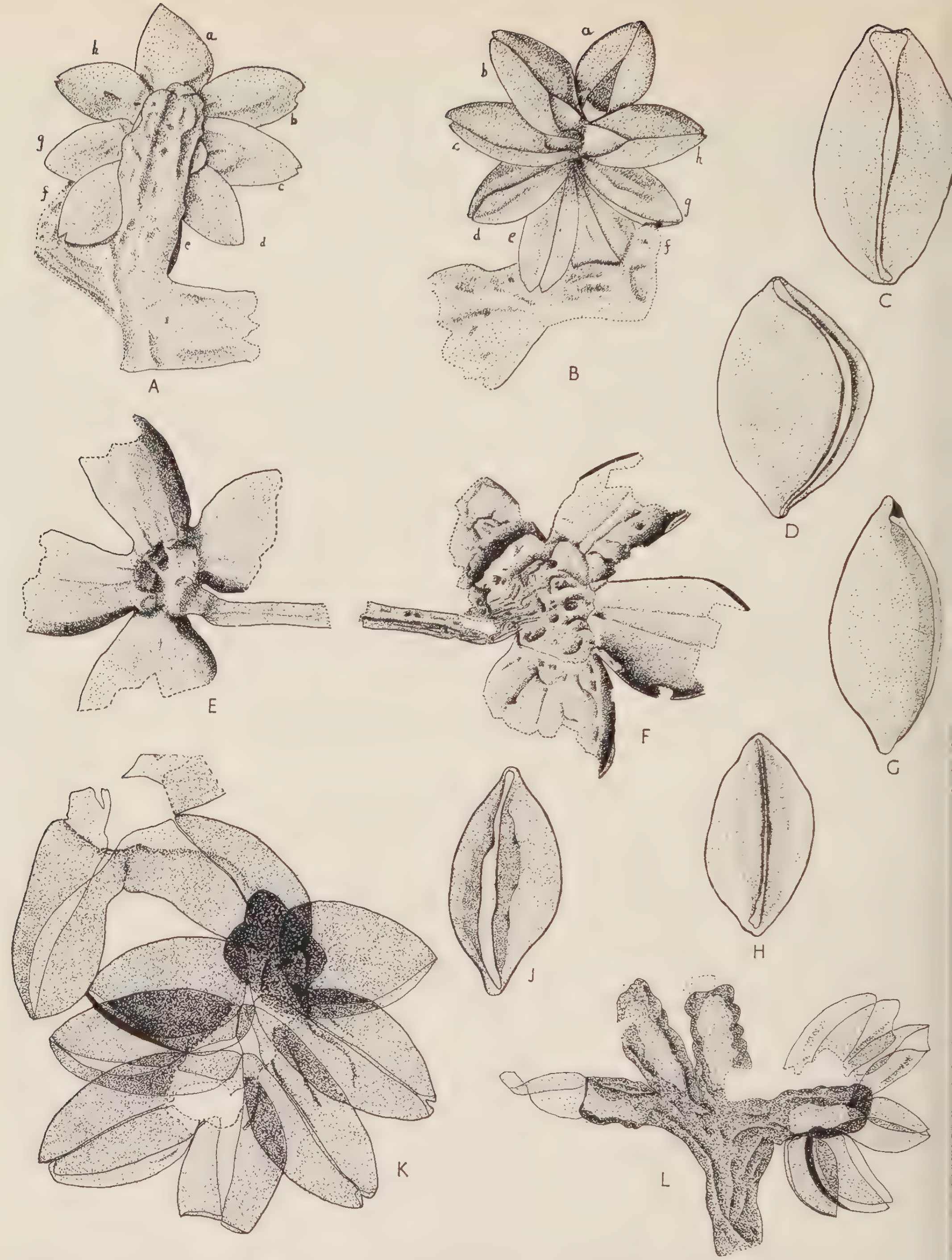
Antevsia zeilleri (Nathorst) Harris

Plate 58, fig. 10; text-figs. 7A–D, K, L; 8E, F, J, K; 9E

1910 *Antholithus zeilleri* Nathorst, pp. 20–24; pl. 2, figs. 59, 60; pl. 4. Type specimen pl. 4, fig. 1; Swedish material.

1914 *Antholithus zeilleri* (Nathorst); Antevs, pp. 10–15, pl. 3 (except figs. 17, 18). Nathorst's material redescribed.

1922 *Antholithus zeilleri* (Nathorst); Johansson, p. 28, pl. 1, figs. 11–13. Additional Swedish material.



TEXT-FIG. 7. A–D, *Antevsia zeilleri*. A, B, Specimen figured by Nathorst, 1908, pl. 4, fig. 1, showing the two surfaces of the organ (A upper, B under); ×7·2. C, D, two pollen grains, area of darker cuticle interpreted as the internal cuticle of furrow; ×875. K, Macerated specimen showing pairs of pollen sacs and fragment of branchlet (dark); ×14. L, A specimen showing four fertile branchlets, one showing lateral bulges clearly, another retaining its pollen sacs; ×7·2. E–J, *A. extans*. E, F, Fertile branchlet ending in disk and four dehisced pollen sacs, E upper side, F lower side (in transfer). F, Lit from bottom right; ×7·2. G–J, Three pollen grains, area of darker cuticle as in C, D; ×875.

1932 *Lepidopteris ottonis* (*Antholithus zeilleri*) (Nathorst); Harris, pp. 62–65, pl. 7, figs. 1, 2, 10, 11; text-figs. 27E, F. Abundant Greenland material.
1937 *Antevsia zeilleri* (Nathorst) Harris, p. 35, diagnosis.

Description. The second species of *Antevsia* raised questions that made a re-examination of the type species desirable, and the Director of the Paleobotaniska Avdelningen, Naturhistoriska Riksmuseet, Stockholm, kindly lent me Nathorst's material.

The whole organ is bipinnate, about 9 cm. long, the rachis bearing alternate branches in one plane about 1·5 cm. apart; these then divide, in a plane more or less at right angles to the rest of the organ, into two to five ultimate branchlets. The rachis and branches show blisters, but the branchlets do not.

The sterile region of the branchlets is 1·5–2·0 mm. wide, and was probably thick in life, for the cuticle shows irregular wrinklings, presumably arising during compression (text-fig. 7L). The cuticle of the two surfaces differs slightly in thickness, and in cell pattern (text-fig. 8E). The fertile region is the same width, or very slightly wider than the sterile part, and the cuticle is only slightly different (text-fig. 8K); stomata number about 20 mm.^{2}, and in four out of six specimens the cells were papillate. The margin of the fertile region is usually produced into a number of bulges, which lie more or less opposite to one another, and are 0·25–1·0 mm. wide, and the same high (text-fig. 7A, B, L). These lobes now appear to be of the same thickness as the branchlet, and the cuticle on *both* their sides is as in text-fig. 8F.

The pollen sacs lie in two rows up the under side of the branchlet end, as preserved from 0·25–0·5 mm. in from the margin. They tend to lie in opposite pairs, one pollen sac to each lobe, but this is not entirely regular, and there is sometimes an unpaired terminal pollen sac. They commonly overlap laterally, and the inner faces of the pollen sacs approximate, so that there is very little, or no, discernible tissue of the branchlet between them (text-fig. 7A, B, K, L). Near the pollen sac's outer edge the cuticle of the lateral bulge shows a varying number of cell rows whose orientation is the same as on the pollen sac itself. There is usually a strong fold, interpreted as caused during fossilization, at the apparent junction of the lateral bulge and pollen sac. These features are much the same whether the pollen sacs are dehisced or not. I suggest that they show that the pollen sacs were borne wholly on the under surface of the branchlet, and that the sides of the thick branchlet overlapped the line of insertion of the pollen sacs.

The bluntly pointed pollen sacs measure about 2 mm. long and 1 mm. wide. The dehiscence slit runs all the way up the inner face to just below the tip on the outer face (text-fig. 9E) and at this point the cuticle commonly shows a little group of equidimensional cells on which the cell rows on the rest of the pollen sac converge. The pollen-sac cuticle is strongly dorsi-ventral. Near the dehiscence line it is thick, showing markedly elongated cells (text-fig. 9E), and opposite to the dehiscence line there is another area of thick cuticle showing roughly rectangular cells ($54 \times 25\ \mu$), but at the base one or two strips of markedly elongated cells, about four cells wide and thirty high (text-fig. 8J), and a few stomata (cf. text-fig. 8G). Between these areas the cuticle is thin, showing elongated cells ($61 \times 19\ \mu$). The outer face of the unmacerated pollen sac is sometimes raised in the area opposite the dehiscence line, and in one or two cases (text-fig. 7A) there is a suggestion of a small mid-rib. The cell rows sometimes converge slightly towards the pollen-sac base, suggesting that the base was slightly contracted.

Four pollen sacs were still filled with pollen, and several others contained some grains. All these grains were alike and no others were seen (Pl. 58, fig. 10; text-fig. 7C, D). When the grains lie sulcus uppermost a curving line can be seen arising at each end of the sulcus (text-fig. 7C) which presumably marks the interior margin of the furrow; while when the grains lie on one side, a further curved line can be seen running under the sulcus (text-fig. 7D), and this I suppose represents the bottom of the furrow. The dimensions of a sample of twenty grains are as follows (extremes in parentheses): length 36·2 μ (46·25 μ, 29 μ); width 22·6 μ (29·8 μ, 20 μ); depth 21·35 μ (26·4 μ, 19·8 μ); interior width of furrow 8·73 μ (13·2 μ, 6·6 μ); depth of furrow 6·3 μ (9·9 μ, 3·3 μ), this value was measured directly from grains lying on their side; the proportions of the grains are: average ratio of length/width 1·6 (1·55 longest grain, 2·3 shortest grain, 1·0 broadest grain, 1·45 narrowest grain); and average ratio of length/depth 1·7 (corresponding figures of extreme specimens, 1·8, 2·32, 1·12, 1·46).

Antevsia extans (Frenguelli) comb. nov.

Plate 58, figs. 4–9; text-figs. 3D, E; 7E–J; 8G; 9A–D; 10A

1927 *Sagenopteris sp.* (non Presl gen.) du Toit, pp. 399–400, pl. 29, fig. 2. Single pollen-sac group; Aliwal North, South Africa.

1944 *Fanerotheca extans* Frenguelli (part), pp. 393–402, pl. 1; pl. 2, fig. 1; pl. 4, fig. 1. (Excluded are pl. 2, figs. 2–4; pl. 3; pl. 4, fig. 2.) Three specimens; near Cacheuta, the Argentine.

?1915 Equisetaceous tubers (?) Walkom, p. 31, pl. 3, figs. 3, 4. Ill-preserved fragments; Denmark Hill, Ipswich, Queensland.

Diagnosis (emended). (Main rachis unknown) presumed branches twice pinnate, ultimate branchlets 0·5–1·0 mm. wide expanding to 2·25 mm. at their ends and bearing four radially arranged pollen sacs. Pollen sacs attached partly marginally and partly on (presumed) under surface, when dehisced about 5 mm. long and 2 mm. wide. Cuticle 1 μ thick or less, on upper surface of branchlet end showing equidimensional cells, stomata, and trichome bases, between pollen sacs showing elongated cells only.

Description and discussion. The material consists of five specimens from the Waterfall locality (see p. 340), and one, v/20796 (Brit. Mus. (Nat. Hist.)), from an unknown locality in the Argentine. The most complete specimens (Pl. 58, fig. 7) show alternate branching. The larger branches show small blister-like swellings, but the branchlets cellular striae only. The cuticle shows trichomes, trichome bases sometimes proliferated, and stomata like those of *L. stormbergensis* (see text-figs. 3D, E; 9B). On the larger branches the

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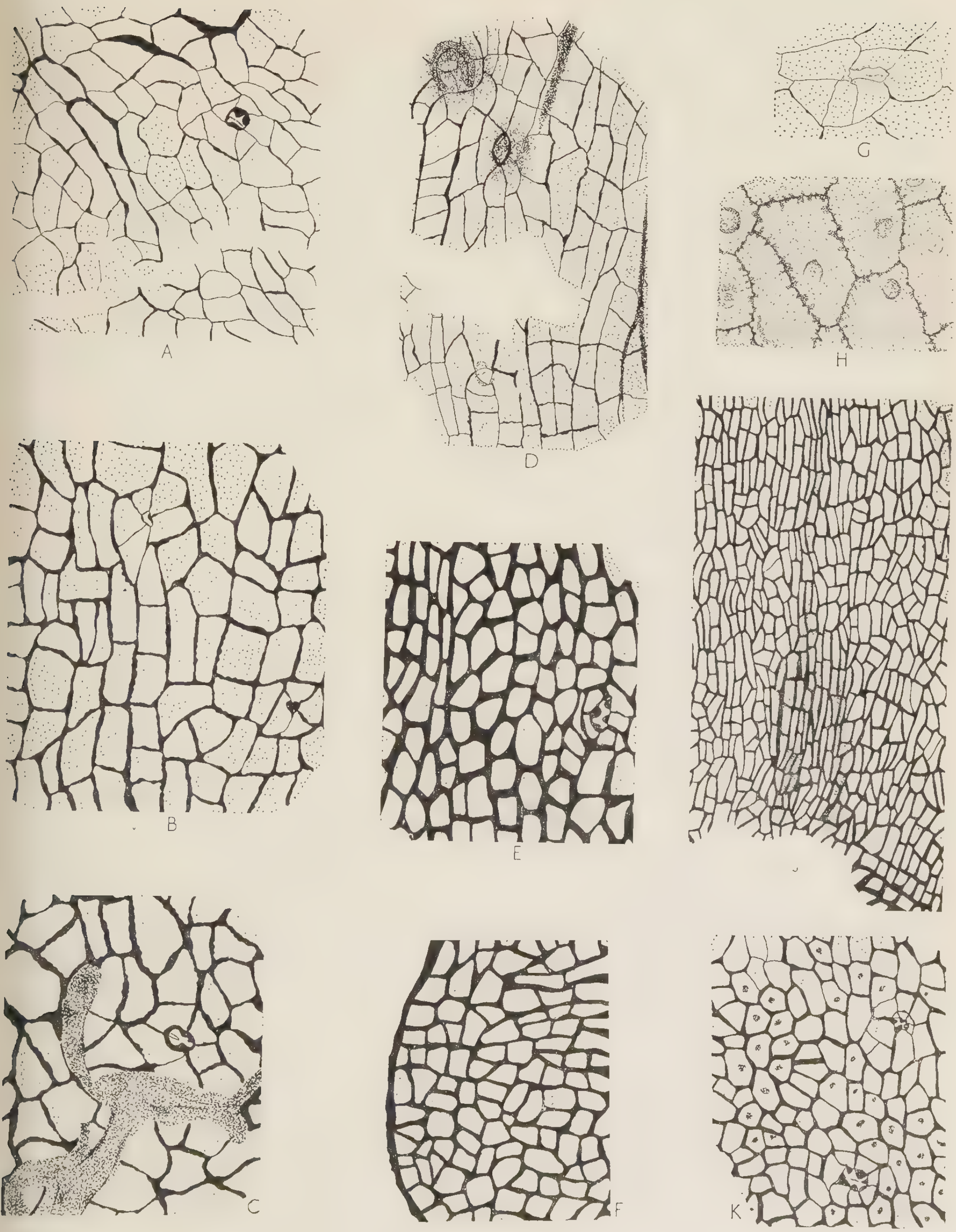
TEXT-FIG. 8. A–D, *Peltaspermum thomasi*. A, Cuticle of outer surface of marginal lobe, showing elongated cells possibly marking the course of a vein. (*Note*: the specimen was torn, and slightly rotated, in preparation); ×167. B, C, Cuticle of upper and lower surfaces of seed head (B lower, C upper), showing cell outlines and stomata. In B darker area of rectangular cells marks course of a vein: in C stippled area marks a fold in which cells are not visible; ×167. D, Cuticle of main rachis showing stoma and two trichome bases, one with proliferated cells; ×167 (A–D all v 23400). E, F, J, K, *Antevsia zeilleri*. E, Cuticle from ultimate branchlet, a part without pollen sacs. F, Cuticle from under surface of a lateral bulge, note cells at top right are similar in shape to the cells at bottom right in J; E, F ×167. J, Cuticle at pollen-sac base, showing elongated cells over mid-rib (centre), and cells probably of branchlet (bottom right); ×88. K, Cuticle from upper surface of ultimate branchlet from a place with pollen sacs on lower surface; ×167. G, *Antevsia extans*, a stoma from a pollen sac; ×327. H, *Lepidopteris stormbergensis*, cell outlines showing form of the sinuosities and papillae; ×327.


A
D
G
H
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K

cuticle is of a different thickness on the two sides, and in the largest specimen the pollen sacs were all the same way up—with the dehiscence line hidden by the rock. This side corresponds to the branch surface with thicker cuticle, so I suppose the pollen sacs were borne with the dehiscence line facing downwards.

The ultimate branchlet is expanded at its apex, and this part is termed the disk Viewed from the upper side the branchlet lies at a lower level than the disk surface and cellular striae cannot be traced from one on to the other: but viewed from the under surface, the disk surface and branchlet lie at the same level, and the cellular striae continue from one on to the other. The branchlet therefore was attached partly to the under surface of the disk as well as to its margin (Pl. 58, fig. 9; text-fig. 7E, F).

Viewed from the under side the edges of the open pollen sacs meet laterally and at the same level (Pl. 58, fig. 8; text-fig. 7F) and radiate out from the disk. Viewed from the upper side the pollen sacs and disk are in complete continuity, and though the centre of the disk is collapsed (presumably it was thick) it is not possible to see where the pollen sac ends and the disk begins (Pl. 58, fig. 8; text-fig. 7E). Supposing that the empty pollen sacs were supported by the matrix during compression (Walton 1936) the union of the pollen sacs and disk lies at the edge of the collapsed region. These appearances mean that the pollen sacs were borne partly marginally and with part of their area of attachment on the under surface of the disk. It seems clear that they were not borne wholly on the under surface of the disk.

The cuticle of both surfaces of the disk are shown in text-fig. 9B, C. Both surfaces show irregular wrinklings, and solitary trichomes were present on the upper surface One pollen sac shows the cells of its interior surface clearly. Other pollen sacs are similar though less clear. Along a thicker rib running for about half the length of the pollen sac (here termed the mid-rib) the cells are elongated, and the other cell rows diverge from it (text-fig. 9A). The cuticle of the pollen sacs (text-fig. 9B) is very delicate, and the cells obscure, partly owing to wrinkling of the cuticle, but the cells over the mid-rib are plainer and more elongated than the others. A few stomata are scattered over the outer face of the pollen sacs, mostly near the mid-rib (text-figs. 9B; 3E). Most of these stomata show neither radially disposed subsidiary cells, nor cutinized papillae. There is no sign of an interior cuticle. The whole pollen-sac wall is of dense substance, and only translucent in one or two places next to the dehiscence slit; in one place the pollen-sac wall is now 0·2 mm. thick.

No unopened pollen sacs were available as a source of uncontaminated pollen, but there were pollen grains adhering to the macerated pollen sacs. Of these forty-six were from 23 to 40 μ long and of one sort, eight were well over 40 μ long, but of the same sort, while three were clearly different. I accept only those grains from 23 to 40 μ long as belonging to *A. extans*, though it is possible that the larger grains belong also. The form of the grains is shown in Pl. 58 and text-fig. 7G–J. They show the same features as *A. zeilleri* and are interpreted in the same way. The dimensions of a sample of twenty grains are as follows: length 31 μ (35 μ and 23 μ); width 17·5 μ (23 μ and 13 μ); depth 16 μ (24 μ and 12 μ); interior width of furrow 8 μ (5 μ and 12 μ); depth of furrow 3 μ (5 μ and 1·6 μ), this last value I regard as rather unreliable as it was taken from ten grains only. The proportions of the grains are: length/width 1·7 (1·8, 1·7, 2·2, 1·4) and length/depth 1·6 (1·8, 1·5, 2·3, 1·4).

Du Toit's pollen-sac group (see Pl. 58, fig. 6) is identified with the present material, for it shows the same form of pollen sac, disk, and branchlet, and the dimensions agree. No microscopic detail was available to du Toit. Frenguelli's material also agrees with the present in dimensions, in showing blisters on the larger branches, and, rather obscurely, a disk to which the pollen sacs are attached (text-fig. 10A) and possibly a median rib. No microscopic detail is given. The specimens quoted above as distinct differ; I believe they belong to another plant, but here discuss them no further.

Discussion of Antevsia. The main rachis of *A. extans* is unknown, so that the two species can only be compared as regards their lateral branches, branchlets, pollen sacs, and pollen. The pollen sacs of both species are strikingly alike. The walls are massive, and the presence of stomata (a most unusual feature) suggests that photosynthetic tissue may have been present. Both species show a mid-rib. The nature of this structure is unknown, but it shows those characters which in compressions indicate vascular tissue; a strand of thicker substance, and epidermal cells modified in shape over it. The pollen of the two species is indistinguishable. I can find no difference in form and an effort to separate the two statistically (sample of 46 grains of *A. extans* and 50 of *A. zeilleri*) failed since the Standard Error of each sample was greater than the difference between the Means.

These resemblances are held to justify the inclusion of both *A. zeilleri* and *A. extans* in one genus.

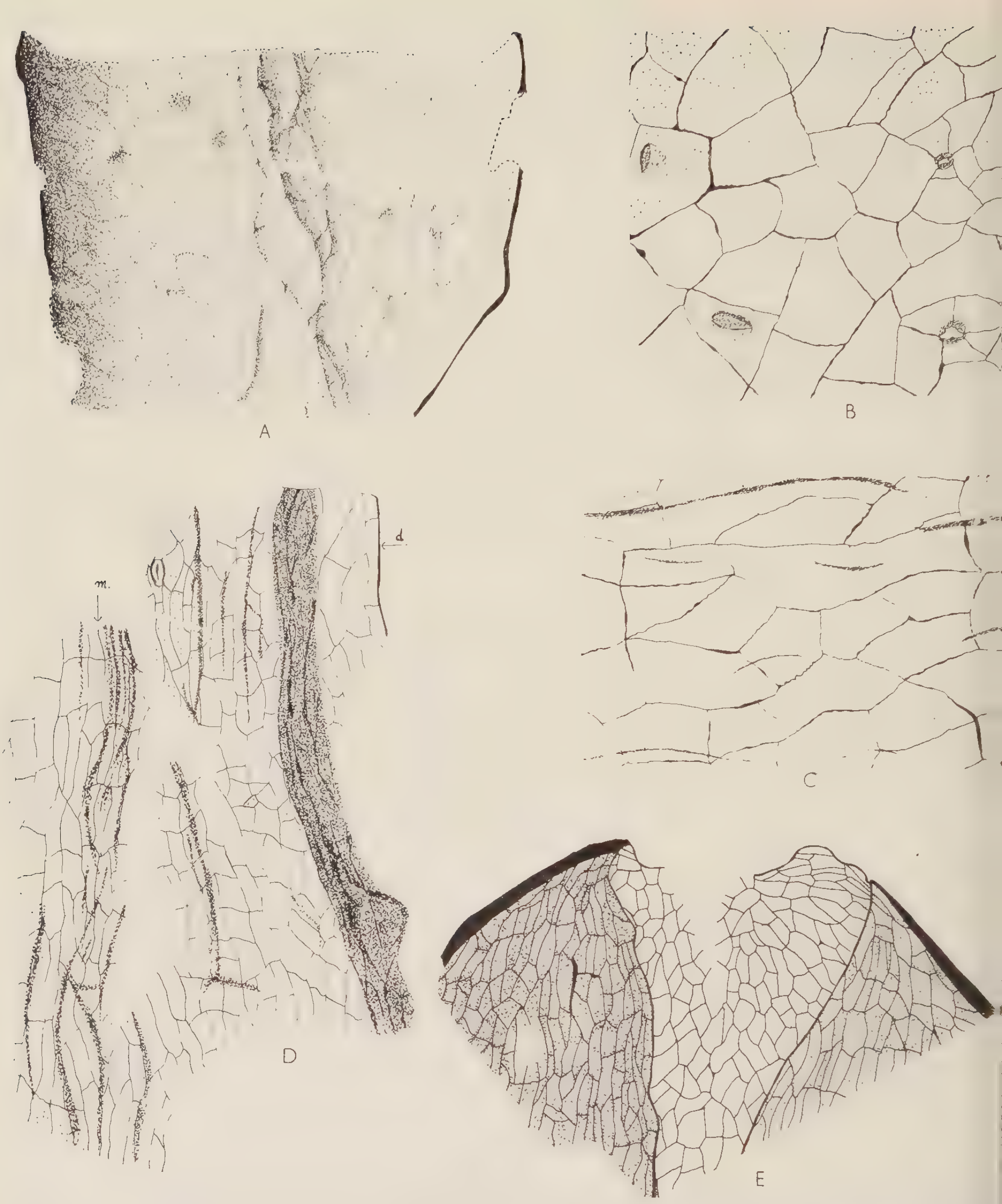
The differences lie in the number and the manner in which the pollen sacs are borne (p. 349 and see text-fig. 7). These differences I regard as variations on a common plan, and they can be explained away in at least three ways. Either we may regard *A. extans* as arising from *A. zeilleri* by specialization of the fertile part and reduction of the pollen sacs to four—perhaps two pairs; or *A. zeilleri* can be regarded as derived from *A. extans* either by amplification in the number of pollen sacs, or by the condensation of several fertile apices of *A. extans* to form one fertile apex of *A. zeilleri*. All three alternatives have to face considerable difficulties, and I do not think it is possible at present to make a choice between them.

Antevsia does not closely resemble other known Mesozoic pollen organs. Two show some approach, *Sphenobaiera furcata* (see Krausel 1943, 1955) and *Antholithus wettsteini* (see Krausel 1955), but both differ in the shape and number of pollen sacs at each fertile apex, and apparently in the construction of the pollen-sac wall and stomatal construction. The isolated pollen grain *Monosulcites minimus* Cookson (see Couper 1953, 1958) is, in figures, indistinguishable from the pollen grains of *Antevsia*. *M. minimus* is an artificial assemblage ranging the Mesozoic which cannot in Couper's opinion be subdivided as yet.

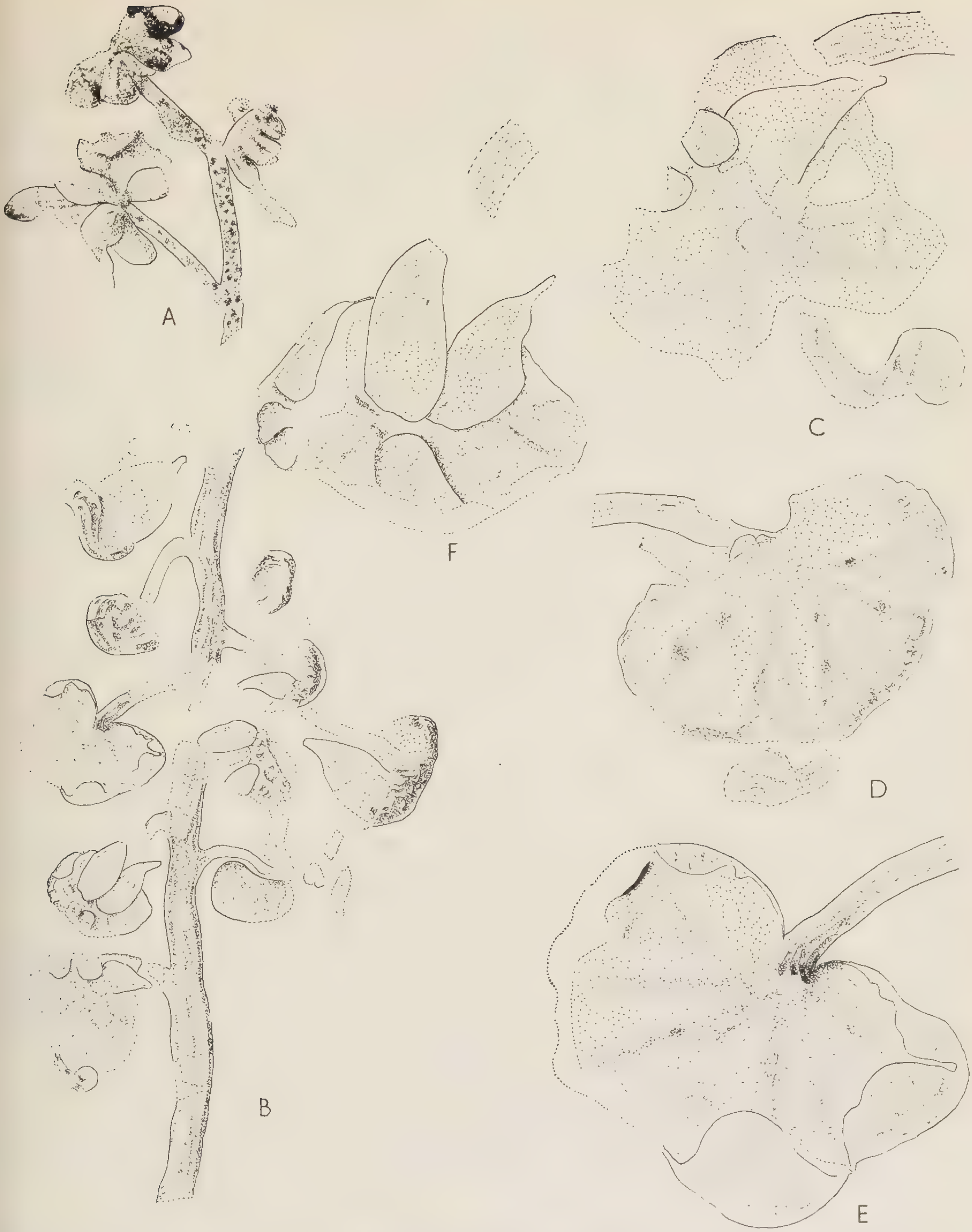
PELTASPERMUM Harris 1937

Type species *P. rotula* Harris

Diagnosis (emended). Whole organ with alternate branches in one plane. Seed-bearing heads borne at branch ends, of thick substance, showing five to fifteen (probably vasculated) marginal lobes over arching surface of head bearing the seeds. Rachis and branches showing blister-like swellings, upper surface of seed head similar. Seeds borne on lower surface of head, either two, lateral to insertion of branch (*P. thomasi*), or ten to twelve in a ring around insertion of branch (*P. rotula*). Cuticle showing stomata of *Lepidopteris* sort. Seeds (*P. rotula* only) with prominent micropyle and free nucellus.



TEXT-FIG. 9. A–D, *Antevsia extans*. A, Interior of pollen sac in transfer, showing cells and mid-rib ×156. B, Cuticle of upper surface of disk showing cells, two stomata, and two trichomes; ×167 C, Cuticle of lower surface of disk; ×167. D, Cuticle of pollen sac, a fold to right, two stomata *d*—dehiscence line, *m*—midrib; ×156. E, *A. zeilleri*. Cuticle at apex of pollen sac showing cells along the dehiscence line and equidimensional cells near apex; ×100.



TEXT-FIG. 10. A, *Antevsia extans*. Specimen from the Argentine, showing branching (redrawn from Frenguelli 1944, pl. 1, fig. 1); ×1. B–F, *Peltaspermum thomasi*. B, The part of type specimen, showing pinnate arrangement of branches; ×6. C, D, First seed head on left showing seed-scar (C on left), seed, veins, and two marginal lobes (part and counterpart; the detached object is of unknown nature); ×9. E, Third seed head on left of part, showing four marginal lobes and veins (the other lobes are broken off); ×9. F, Second seed head on left of part, showing two seeds and three marginal lobes; ×9. All from v/23400.

Peltaspermum thomasi Harris

Plate 58, figs. 2, 3; text-figs. 3F; 8A-D; 10B-F; 11

1933 *Lepidopteris natalensis* Thomas (in part only), pp. 251, 254, pl. 24, fig. 75; text-fig. 55. Type specimen described (under same name as leaf).
1937 *Peltaspermum thomasi* Harris, pp. 34–35. Diagnosis.

Diagnosis (emended). Main rachis showing small blisters and lateral wing; seed-bearing heads attached marginally, showing five or six marginal lobes, and pinnately branched veins on lower surface; interval between veins about 0·5 mm. Seeds two per head, attached laterally to branch insertion, about 3 mm. long and 1·5 mm. wide.

Description. The material consists of the type and two other specimens (v/23400. v/35798, and v/35799, Brit. Mus. (Nat. Hist.)), all from the Burnera Waterfall locality. The type was described by Thomas (1933), but my interpretation differs from his.

In v/23400 the specimen is compressed on one bedding plane, but the others traverse several, and probably preserve the original shape of the organ more nearly. Upon this view the seeds pointed down towards the base of the organ. The cuticle of one side o the rachis is thicker than the other, and this suggests that the organ may have bee upright or inclined rather than pendulous.

The rachis and branches have a cuticle like that of *L. stormbergensis*, showing trichomes stomata, and a wing (text-figs. 3F; 8D). Though not all are clearly shown the evidence is fully consistent with the view that the branching was pinnate, for the wing on th branches is decurrent on to the wing on the rachis without sign of twisting in the ce rows (Pl. 58, fig. 2; text-fig. 10B). Like the pinnae of the leaf the branches are attache towards one (presumably the upper) surface of the rachis (text-fig. 11A).

The round or cordate seed-bearing heads are attached at one edge and not in th middle. The lower epidermis of the branch passes gradually into the lower epidermis o the head, and the upper into the upper epidermis of the head, but most of the attachmen lies on the lower surface of the head, so that head and branch do not lie at the same leve (text-fig. 10D, E). The whole head is of thick substance, and its upper surface is raised in irregular wrinkles, especially towards the margin, but at the extreme margin there is a flat rim about 0·5 mm. wide (text-fig. 10D, E). Presumably, therefore, the whole hea was thick, or dome-shaped, and the flat rim is a compression border (Walton 1936) At the margin of the heads, lying just inside the compression border (text-fig. 10C, E, F), there are semicircular lobes, about 1 mm. high at a maximum. In one head (text-fig 10E) there were six occupying the whole circumference. The cuticle of the lobes is similar to the cuticle of the head, and there are no internal cuticles, or signs of a micropyle, so that they cannot be seeds. The arrangement of epidermal cells (text-fig. 8A) suggests the lobes may have been vasculated, and there appear to be as many lobes as veins in the head.

The lower cuticle of the heads is only broken by the seeds, and by scars believed to mark the insertion of seeds. Three heads show clearly (text-fig. 10C–F) a system of raised lines, over which the cells are elongated, and which on incomplete maceration show a strand of dark substance (text-fig. 8B). These lines are therefore veins. The cuticle of the upper surface of the head is shown in text-fig. 8C.

In two heads there are two seeds lying laterally to the branch insertion, and more or less over the first dichotomy of the vein (text-fig. 10F). In another head only one seed was present, but there is a scar in the corresponding position (text-fig. 10C). In the other heads there is one seed shown. I suggest that two seeds per head is probably the normal.

The seeds (which may not be mature) are about 3 mm. long and 1·5 mm. wide, with a micropyle which is slightly curved away from the branch. I have not macerated any seeds, since there are so few.

Discussion of Peltaspermum. The two species of *Peltaspermum* are superficially rather different. *P. rotula* has peltate radially symmetrical seed heads, 10–12 seeds, and 10–15 marginal lobes: *P. thomasi* has bilaterally symmetrical seed heads, attached marginally, 2 seeds and 5 or 6 marginal lobes. Nevertheless, the two species appear to be organized on the same plan, so they are left in one genus. Thus the seed heads of *P. rotula* were unattached, but there is evidence that they were borne in two rows on a central rachis (Harris 1932, p. 66). The seed heads of *P. rotula* were certainly thick (Harris 1932, pp. 65–66), and I suggest that the rim shown in Harris's reconstruction is a compression border. This is supported by the appearance of some Swedish material of *P. rotula* (Lundblad 1950) which is preserved 'in the round'. Lundblad found that in her Swedish material there were as many ridges between the seeds as marginal lobes (cf. also Harris 1932, pl. 8, figs. 1, 2, 9), while the cuticle of the lower surface of the heads is stated to consist of elongated (rectangular or polygonal) cells. Lundblad's discovery suggests that, as in *P. thomasi*, the lobes may have contained vascular tissue which continued within the head, between the seeds.

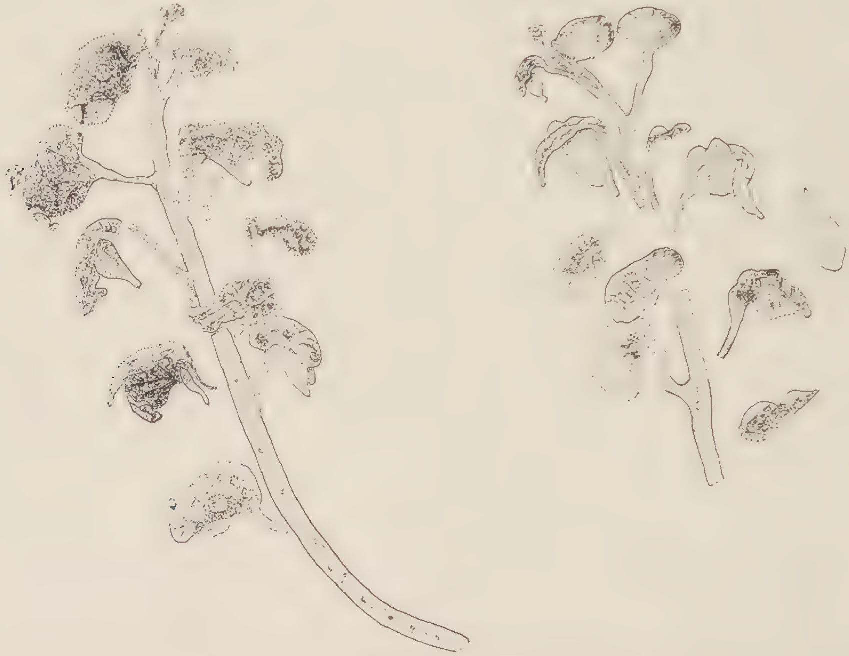
GENERAL DISCUSSION

(*a*) *Reference of isolated organs to the parent plant. Lepidopteris ottonis*, *Antevsia zeilleri*, and *Peltaspermum rotula* are all referred to the same plant because they all show blisters on their rachis cuticles and the same sort of stomata, two features not found together in other plants of the holoarctic Rhaetic floras. In addition, leaf, pollen, and seed organ are found together in several localities in Greenland and Sweden, and in some of these *L. ottonis* is the local dominant (Harris 1932; Lundblad 1950).

The same arguments are applied to *Lepidopteris stormbergensis*, *Antevsia extans*, and *Peltaspermum thomasi*, and as far as I know no other plant in their flora shows the combination of blisters and stomata of the *Lepidopteris* sort. Evidence from association is weaker than in the case of the *L. ottonis* plant. If the identifications suggested hold, *L. stormbergensis* and *A. extans* are found together in three localities, the Waterfall, near Cacheuta, and Aliwal North; but other plants are also common to these three localities. *P. thomasi* is known only from the Waterfall. However, the evidence for relationship between the *L. ottonis* and *L. stormbergensis* plants automatically supports also the reference of each isolated organ to its parent plant.

(*b*) *The Morphology of* Antevsia *and* Peltaspermum. Previous authors (e.g. Harris 1932; Thomas 1932; Hirmer 1939; Frenguelli 1944) have considered *Antevsia* to be a microsporophyll. I agree, taking 'sporophyll' to mean an organ that is like a leaf, but not pursuing the question of the ultimate meaning of the term. *Antevsia* shows pinnate branching like a compound leaf, and not spiral or whorled branching like a stem. The organ also is flattened in one plane, at least as regards the first branching.

Likewise, I think that *Peltaspermum* is a sporophyll (but see Thomas 1933). *P. thomas* is flattened in one plane, and shows pinnate branching like the leaf; and probably *P* *rotula* is similar. The seed-bearing heads of *P. thomasi* are bilaterally symmetrical, and show a pinnate plan of venation. *P. rotula*, however, is unique (see Harris 1932; Hirme 1939; Lundblad 1950), but is referred to the youngest member of the family, and suggest that the form of its seed heads can be regarded as secondary and derived, jus as peltate Dicotyledonous leaves are regarded as derived.



TEXT-FIG. 11. *Peltaspermum thomasi.* Part (A) and counterpart (B); v/35798; ×3.

Peltaspermum thomasi can be compared with the multi-ovulate cupule *Gnetopsis* *elliptica* Renault 1885 (and see Walton 1949), for they are about the same size, and the basic construction of the seed-bearing portions appears to be similar. There are important differences; for example, *G. elliptica* has seeds which somewhat resemble *Lagenstoma* (see Oliver and Salisbury 1911). This similarity between *Gnetopsis* and *P. thomasi* strengthens Harris's (1932) suggestion that *Peltaspermum* is best regarded as a multi-ovulate cupule (for a discussion of the cupule see, for example, Halle 1937; Walton 1949); and makes it improbable that the seed heads of *Peltaspermum* are more or less unmodified pinnules such as bear seeds in some pteridosperms (see Halle 1929, 1931).

(*c*) *The relationships of the Peltaspermaceae.* As they are interpreted, the Peltaspermaceae resemble the Pteridospermae (= Cycadofilicales) and no other group of gymnosperms. They show no particular approach to the other groups of (presumed) pteridosperms in the Mesozoic, the Corystospermaceae (Thomas 1933) and *Harrisia marsilioides* (see Lundblad 1950) with its leaf *Ptilozamites*. Gothan and Weyland (1954) have classified the Peltaspermaceae with the Caytoniales (probably having affinities with pteridosperms, see Harris 1951), but the only similarity is that both groups have reproductive organs built on a pinnate plan.

Among Palaeozoic pteridosperms, the Peltaspermaceae show one distinct point of resemblance to the Lyginopterideae, namely that two vascular traces enter the leaf base which then unite. This is quite different from the structure of the medulloseaen petiole.

The leaf *Lepidopteris* shows some interesting similarities with the leaf *Paripteris* Gothan (1941, 1953). In both the rachises are blistered (text-fig. 4J, K, and Gothan 1941), though the structure of the blisters in *Paripteris* is not known; in both there are zwischerfiedern, which continue on to the abaxial leaf surface, where they may form tufts (text-fig. 4J, K, see Bertrand 1930); and both have stomata typically surrounded by radially disposed subsidiary cells (text-fig. 6E). None of these features appears to be very common among fossil leaves, and, so far as I can discover, no other leaves show the combination. There are differences; *Paripteris* is at least tripinnate, paripinnate, and of neuropteroid pinnule form and venation.

The reproductive organs of *Lepidopteris* cannot be closely compared with any known Palaeozoic pollen or seed organ. *Antevsia* has been tentatively compared with *Urnatopteris* (see Harris 1932) and *Crossotheca* (see Harris 1932; Thomas 1936; Frenguelli 1944), but *Crossotheca* has bilocular pollen sacs (at least in the better-known species) partly adnate to the 'fertile pinnule', and round pollen grains without a sulcus but with a triradiate mark (see Kidston 1906, 1923; Florin 1937; Remy 1955). *A. extans* can be visualized in terms of a *Potoniea* in which the pollen sacs have been reduced to four and the 'fertile pinnule' to the disk (see Halle 1933; Florin 1937; Remy 1955), and this comparison gains force slightly since *P. adiantiformis* has been found in organic connexion with *Paripteris gigantea* (Gothan 1913). But the differences in form between *Potoniea* and *Antevsia* are great, and the pollen is different. The isolated Rotliegend fossil *Pteridospermostrobus gimmianus* Remy (1954) appears to have a structure a little like *Antevsia*, but its pollen is quite different from *Antevsia*.

Gnetopsis elliptica is the only fossil that appears to be at all like *Peltaspermum*; it has only been found isolated, and its affinities are uncertain, though it is not medulloseaen.

Among the Pteridospermae, therefore, the Peltaspermaceae show one distinct point of resemblance to the Lyginopterideae, and a rather tenuous resemblance to the Potonineae. Nowhere do they show any resemblance to the Medulloseae. They must still be considered a group on their own, but perhaps lying not far from the Lyginopterideae. I can find no support for Thomas's (1932) suggestion that they might show some approach to the Angiosperms.

The earliest record of *Lepidopteris* is from the Thuringian of Europe; the southern hemisphere records are all Triassic. It thus seems more probable that the family originated in the northern hemisphere and spread over the rest of the world from there, than that it is southern in origin.

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JOHN A. TOWNROW,
Botany Department,
University of Reading

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PHOTONEGATIVE YOUNG IN THE TRIASSIC LAMELLIBRANCH *LIMA LINEATA* (SCHLOTHEIM)

by R. P. S. JEFFERIES

ABSTRACT. The occurrence of young specimens of *Lima lineata* (Schlotheim) within the lunules of adults of this German Triassic species is held to be due to photonegative habits and points to a possible origin of nest-building in the Limidae. The non-occurrence of this feature in some parts of Germany and its abundance in other parts is believed to depend on whether or not the adult was byssally attached.

IN the deeply excavated lunules of double-valved specimens of *Lima lineata* (Schlotheim) from the Wellenkalk (Middle Triassic), near Heidelberg and Würzburg, it is common to find one or two double-valved specimens of young of the same species. Two things show that this association is not accidental; firstly the young are nearly always at the extreme anterior end of the lunule—of thirty-nine young observed thirty-two were anterior, six were median (including four which were members of a pair and which were as anterior as the other member of the pair would allow), and only one was posterior; secondly the young nearly always have their lunules pressed close to the floor of the adult lunule (twenty-nine out of thirty-seven determinable cases). The purpose of this note is to discuss this phenomenon.

Seilacher (1954) has shown, from mode of crushing and orientation of attached epizoa that double-valved specimens of *Lima lineata* were usually embedded with the commissure vertical and resting on the antero-dorsal margin (Pl. 59, fig. 7). This orientation which I have seen in two specimens *in situ* at Lengfurt, near Würzburg, was the life-orientation of the species. This is shown by the fact that modern Limidae normally rest in the same position (Studnitz 1931), except when lying at random in the nest, and by the fact that the byssal gape, which is fairly large in *Lima lineata* (Pl. 59, fig. 4), is on the antero-dorsal side.

The elongate antero-dorsal margin of the Limidae is an adaptation to this mode of life and has led to the markedly posterior position of Limid umbones. The antero-dorsal side of *Lima lineata*, in particular, makes a very firm base to rest upon; it is a broad, heart-shaped area (Pl. 59, figs. 1–6) consisting of the excavate, cordate lunule bordered to right and left by rather flat anterior umbonal ridges which have specially coarse radial ribs. When resting on the sea-floor in the position described these anterior umbonal ridges would be the only parts of the shell actually touching the floor and their coarse ornament would help to prevent slipping at the contact. In 1910 Douvillé (p. 645) had already noticed the adaptive significance of the flattened antero-dorsal surface in *Plagiostoma*, in which subgenus *L. lineata* should probably be placed (Philippi 1900, p. 621).

Hence *Lima lineata* rested in life with the lunule downwards. Communication between the sea and the lunule was, nevertheless, possible through the gap between the prominent umbones. It was doubtless through this gap that the young specimens entered. They could scarcely have found their way so commonly into such a small gap, however

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unless they were photonegative with a definite tendency to enter small crannies. And in this connexion it is interesting to find the same photonegative tendency in Recent *Lima* (Crozier 1921). The actual position which the young adopted at the extreme anterior end of the lunule (Pl. 59, figs. 1–5) may also, with light coming from above, have been the darkest place inside the lunule. At least it was clearly the farthest point from the source of illumination. The orientation which the young adopted, with their lunules pressed to the floor (or 'ceiling') of the adult lunule, meant that their relationship with their substratum was the same as that of the adults to the sea-floor and suggests that they were byssally attached.

Before proceeding farther a digression on the habits of Recent Limids is necessary. These fall morphologically into three groups which Pelseneer (1911, p. 32) called *Mantellum*, *Limatula*, and *Radula*. In nomenclature these groups are unsound (*Mantellum* Bolten 1798 = *Lima* Bruguière 1792 (same type species) and *Radula* Klein 1753 is pre-Linnaean (Arkell 1931, p. 128)). From the present standpoint, however, nomenclature is unimportant since the three groups seem to have real existence. '*Mantellum*' (e.g. *Lima hians*) includes forms with extensive gapes round the whole shell margin (except the hinge line); they have the interesting habit of using the byssus to form a sort of nest, usually under stones or inside empty shells. MacGinitie and MacGinitie (1949, p. 346) say of the American species *Lima dehiscens* that it 'builds nests *in cavities* by spinning byssus threads and attaching them to the surrounding rocks in a scattered formation. The completed nest is suggestive of the nest that certain spiders build and in which they wait for their prey.' (My italics.) Studnitz (1931, p. 301) gave a very similar account of nest-building in the European *Lima hians* which usually makes its nest inside empty *Mytilus* or *Cardium* shells. There seems to be no fixational byssus in '*Mantellum*', for Pelseneer contrasts these 'Limes nidificatrices' with the 'Limes à byssus fixateur' represented by '*Radula*'. Pelseneer's second group, *Limatula*, consists of small equilateral forms with a fairly wide byssal gape but no gape round the rest of the shell margin. Little is known of the habits of this group, but there is no evidence of nest-building in the British species *L. subauriculata* (C. M. Yonge, personal communication). Pelseneer's third group, '*Radula*', includes very large species (e.g. *Lima excavata*) with a flattened or excavate antero-dorsal margin and no gape but the byssal gape, with a fixational byssus and without the nest-building habit. '*Mantellum*' can swim by clapping its valves (Studnitz 1931; MacGinitie and MacGinitie 1949) and it is possible that *Limatula* and '*Radula*' can also do so though the habit does not seem to have been recorded.

Now '*Radula*' is very like *Plagiostoma* and, indeed, there is no clear distinction between them apart from age (Philippi 1900, p. 621). By the same token it is '*Radula*', of all Pelseneer's three Recent groups, which *Lima lineata* most nearly resembles. It is similar in its large size, excavate lunule, and absence of any gape except the byssal gape; and this comparison suggests that *L. lineata* was not a nest-builder.

There is more direct evidence to the same effect. Seilacher (1954, p. 167) stressed the fact that double-valved *Lima lineata*, which had evidently been buried with commissure vertical, nevertheless had their valves closed. He concluded from this that they must have been buried shortly after death, for on death the ligament would have opened the valves automatically if the shell had been lying free on the sea-floor. This deduction does not seem to go far enough, however, for on death the valves would open at once. To produce fossils with their valves closed burial would therefore have to be simultaneous with death or slightly precede it. In fact it seems likely that double-valved *Lima lineata* found in the life-position with their valves closed were nearly always killed by burial. The same conclusion would not, of course, apply to valves buried with commissure horizontal for these would be closed by weight of sediment.

From this argument it follows that the attached animals on *Lima lineata* (or at least those found on the lower half or two-thirds of an animal killed by only partial burial) must have been attached during the life of the *Lima*. This is confirmed by the presence on one specimen of *L. lineata* (Pl. 59, fig. 7*a*) of a *Lopha sp.* which is truncated against a growth-line of the 'host' and so must have lived when this growth-line represented the edge of the valve. Now attachment of epizoa in such abundance as is usual could scarcely have happened if the *Lima* had been surrounded in life by a nest of byssal threads. The occurrence of *Lopha sp.* in the Muschelkalk has been previously noticed by Seilacher (1954) and Cox (1932).

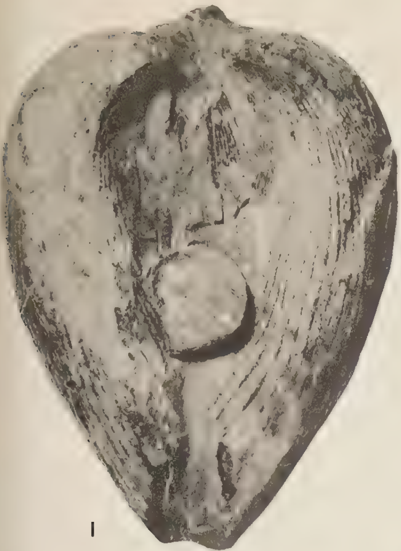
Furthermore, there is evidence of a fixational byssus in *Lima lineata*, which, as pointed out above, probably does not occur in Recent nest-builders. Seilacher (1954, p. 176) noticed that small, single-valved shells of various species were often present in the lunules of his specimens (cf. Pl. 59, fig. 6). Near Freudenstadt (text-fig. 1), from which most of Seilacher's material came, this phenomenon was quite regular (about 30% of specimens). It is clearly different from the attachment of double-valved young in the lunule, for the fact that the shells are single-valved and of many different species proves that they became associated with the *L. lineata* only after their death. Seilacher's explanation, that they represent debris attached to the byssus of the *Lima*, seems the only reasonable one.

EXPLANATION OF PLATE 59

Figs. 1–7. *Lima lineata* (Schlotheim). 1, Antero-dorsal aspect. ×1. Diedesheim. Heidelberg University collection. Note young specimen at extreme anterior end of the adult lunule, oriented with its lunule to the floor of that of the adult. 2, Antero-dorsal aspect. ×0·75. Leimen. Heidelberg University collection. Remarks as for fig. 1. 3, Oblique antero-dorsal aspect. ×0·75. Rohrbach. Heidelberg University collection. Remarks as for fig. 1. 4, Antero-dorsal aspect. ×0·75. Lengfurt. British Museum no. LL8481. This specimen was found *in situ* in the quarry with the antero-dorsal margin downwards. The particularly coarse costation of the anterior umbonal ridges and the byssal gape between the two halves of the lunule are clearly visible. Of the two young individuals in the lunule, one is at the extreme anterior end and the other is as anterior as the first member of the pair would allow. Both have the lunule pressed close to the floor of the adult lunule. 5, Antero-dorsal aspect. ×0·75. Leimen. Heidelberg University collection. Remarks as for fig. 1. 6, Oblique antero-dorsal aspect. ×0·75. Güngrich near Pirmasens. Heidelberg University collection. Note the presence of abundant byssally attached debris at the posterior end of the lunule, and the shallowness of the lunule, possibly due to the persistence of the byssus in the adult. The debris includes two valves of a young *Lima lineata* (at *a*) and a small gastropod *b* as well as other material. The specimen of *Anodontophora fassaensis* (Wissmann) at *c* was probably part of the byssally attached debris but has been displaced by compaction of the sediment. 7, Oblique lateral aspect. ×0·75. Lengfurt. British Museum no. LL8482. This figure shows the specimen resting on the antero-dorsal margin in the orientation in which it was found *in situ*. The epizoa are *Placunopsis plana* (Giebel), *Lopha sp.* and small bryozoa.

Fig. 7*a*. *Lopha sp.* ×2·25. Enlarged view of specimen also visible in fig. 7. Note the truncation against a growth-line of the 'host' which proves that the *Lopha* must have lived when the 'host' was of the size represented by the growth line.

Figs. 1–3 and 5 are by Dr. A. Seilacher and figs. 4 and 6–7*a* are by J. Pope.



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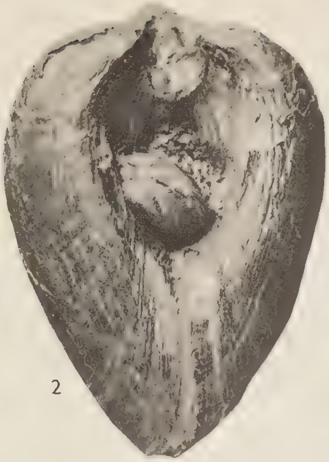

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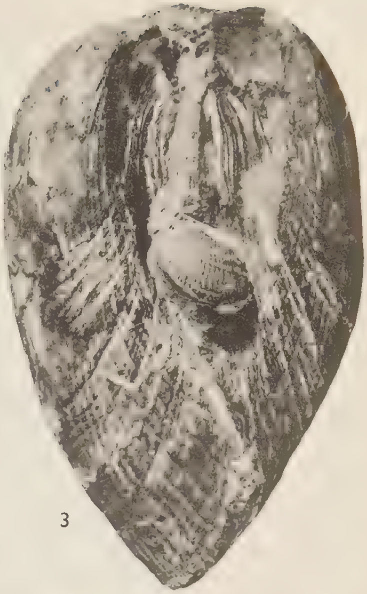

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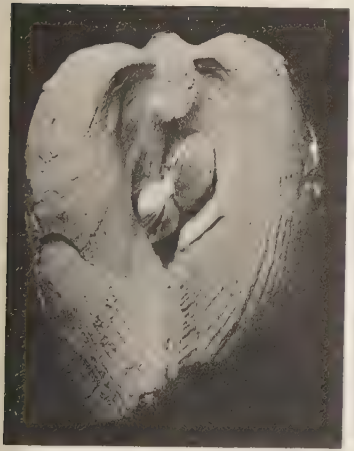

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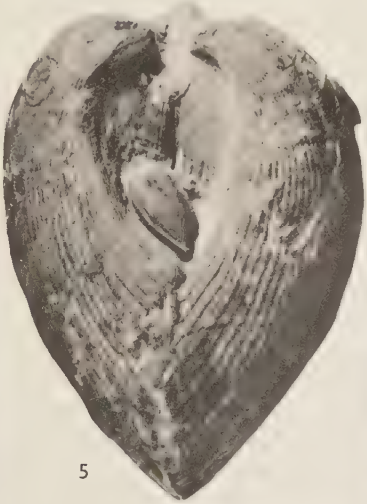

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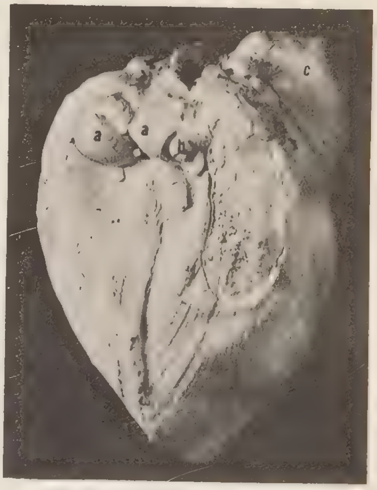

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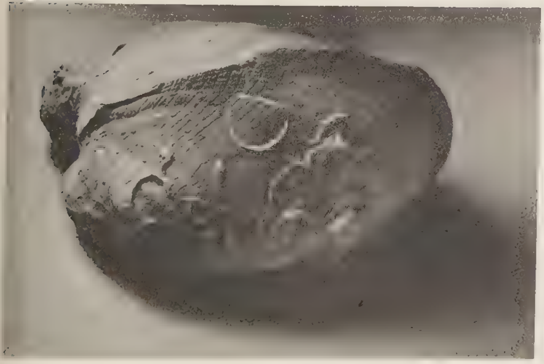

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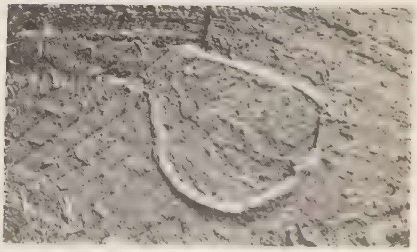
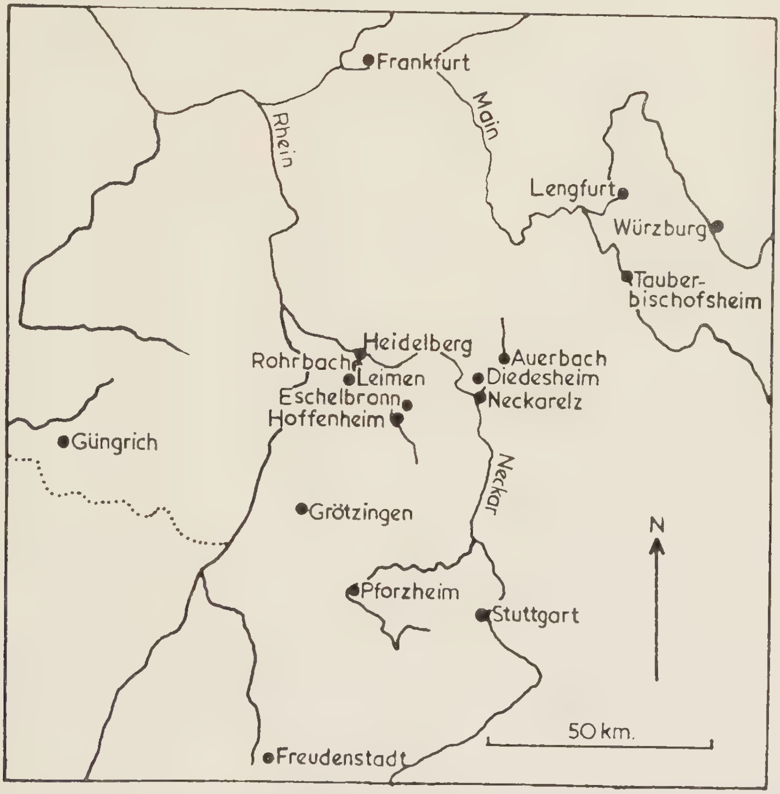


7a

However, though *L. lineata* was probably not a nest-builder, its young had a habit of entering crannies and fixing themselves inside and it was probably from this that the Limid habit of building nests inside cavities arose. This is not to suggest, of course, that *Lima lineata* was the direct ancestor of nest-building Limidae; but if *L. lineata* was photonegative the ancestor of '*Mantellum*' may also have been so.



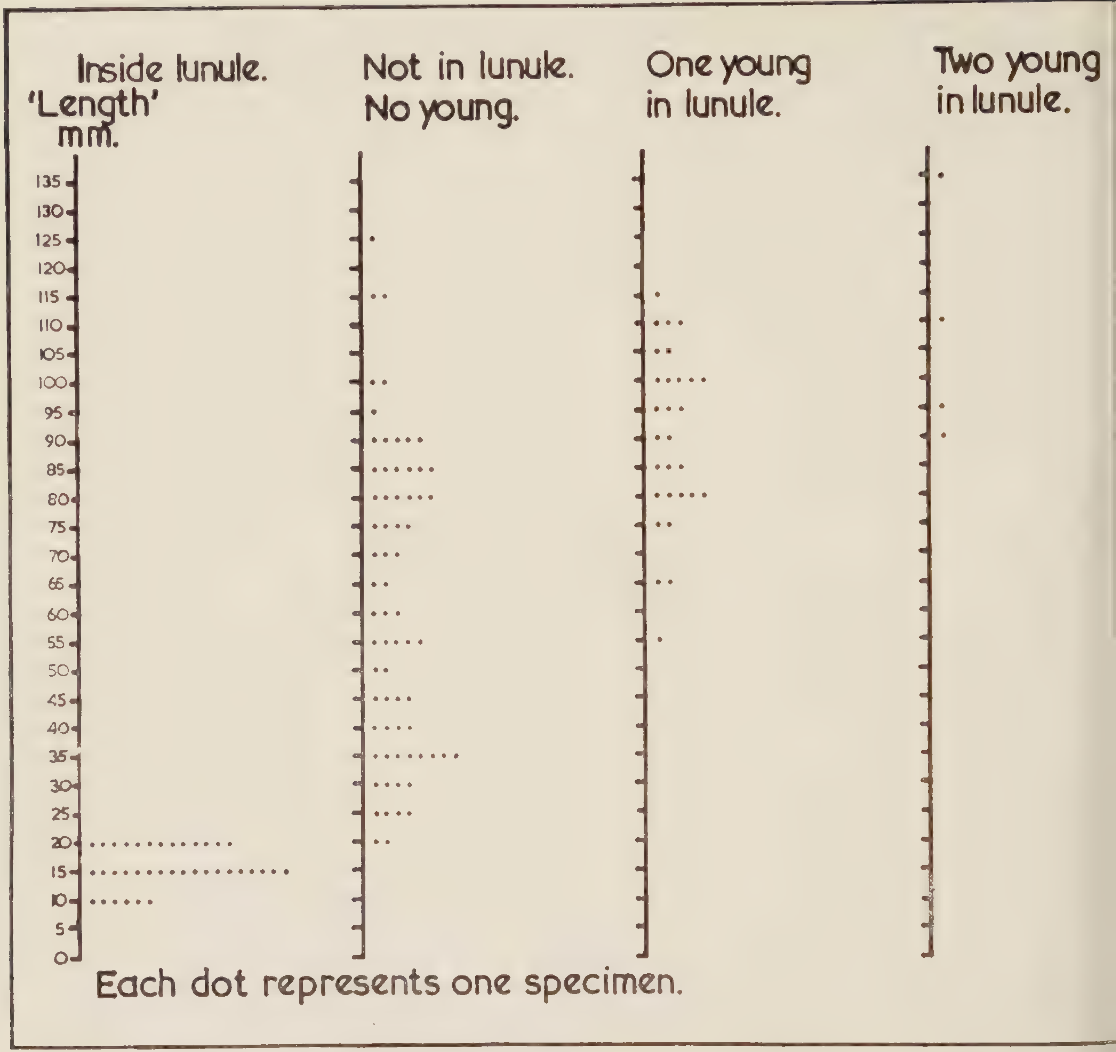
TEXT-FIG. 1. Locality map. Young inside the lunule are abundant near Heidelberg and Würzburg but apparently absent near Freudenstadt. Byssally attached debris, on the other hand, is abundant near Freudenstadt but rare near Heidelberg and Würzburg.

Text-fig. 2 shows the relation between habit and 'length' in *Lima lineata* from the Wellenkalk, near Heidelberg and Würzburg, 'length' being the largest dimension parallel to the antero-dorsal margin. One hundred and one specimens have been used in the construction of the figure (not counting young specimens inside the lunules of other specimens) and their localities of origin are as follows:

(i) Lengfurt near Würzburg, 3 specimens (collected by the author, British Museum numbers LL8481–3).

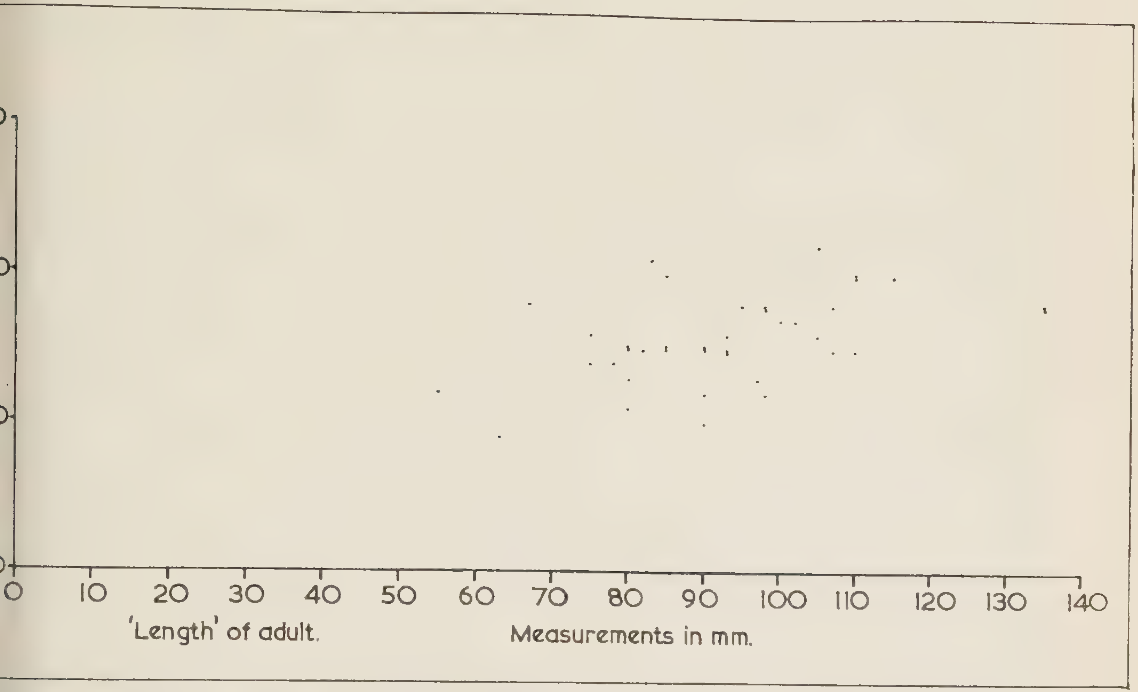
(ii) Leimen, 54 specimens; Diedesheim, 35; Auerbach, 4; and 1 specimen each from Tauberbischofsheim, Neckarelz, Rohrbach, Eschelbronn, and Hoffenheim (in the Heidelberg University collection).

The sample presented in text-fig. 2, as pointed out above, is part of a population which died suddenly. For this reason the age and size distribution of the sample, apart



TEXT-FIG. 2. Distribution of habit with 'length' in *Lima lineata* from the Wellenkalk near Heidelberg and Würzburg. 'Length' is the greatest dimension parallel to the antero-dorsal margin and is plotted to the nearest 5 mm.

from the considerable vagaries of preservation and collection, should be the same as in a living population of the species. It therefore seems legitimate to conclude that in the Heidelberg–Würzburg area a young *Lima lineata* did not try to enter an adult lunule until it was about 7 mm. long. Perhaps below this size it was not photonegative. Although in the figure almost 100% of the specimens between 5 and 20 mm. long are found inside lunules, the percentage was probably very much less in life. Unprotected individuals of this size would probably have been disarticulated after death and so would not have been included in the sample which was purposely restricted to double-valved specimens. Also it is clear that small Limas inside adult lunules would be much more easily trapped by sudden deposition of sediment than would similar individuals living outside. At about 20 mm. the young left the lunules, which had presumably become uncomfortably small. Then, at a length of about 55 mm. or greater, the animals started in their turn to serve as 'host' to young, and this continued till death.



TEXT-FIG. 3. Relationship between 'length' of young in lunule and 'length' of 'host' adult, based on all observed specimens with young in the lunule from the Wellenkalk. 'Length' is the greatest dimension parallel to the antero-dorsal margin.

Text-fig. 3, which is based on all observed specimens from the Wellenkalk with young in the lunule, includes two specimens from Güngrich near Pirmasens besides those used in the construction of text-fig. 2. It shows that the size of a young specimen was related to the size of the 'host', i.e. roughly speaking the adult was six times as large as the associated young. At first this might suggest that a young *Lima* in the lunule of a large 'host' had attached itself when the 'host' was smaller and grown *pari passu* with it. This is probably not the correct explanation, however, for the percentage linear growth-rates of the adults would probably be negligible by comparison with those of the young. It seems more likely that young Limas were capable of leaving a lunule they had outgrown, and that then they either lived free, or found more spacious accommodation.

The fact that Seilacher did not find double-valved young inside the lunules of his specimens from near Freudenstadt proves that they must be very rare there. On the other hand, text-fig. 2 shows that near Heidelberg and Würzburg thirty-three specimens out of a total of seventy-three longer than 50 mm. had one or two young inside the lunule. This is probably linked with the fact that, as mentioned above, 30% of Freudenstadt specimens had byssal debris in the lunule while stray fragments which might represent such debris were present in only four of the seventy-three specimens from near Heidelberg and Würzburg. Even though such debris will often have been removed during preparation the difference is probably significant. It suggests that perhaps the typical adult near Heidelberg lay free on the sea-floor, whereas the typical adult near Freudenstadt was byssally fixed. This is not improbable, for the Wellenkalk near Freudenstadt is of more marginal facies and only half as thick as near Heidelberg and Würzburg (55 m. as opposed to 98 m. (Schmidt 1928, opp. p. 24)) and so the sea near Freudenstadt was probably shallower and more turbulent.

Persistent byssal attachment in the adult might affect the young in two ways. Firstly there would be a mass of byssus and byssally attached debris blocking the gap between the umbones of the adult and making it difficult for the young to enter the lunule. Secondly there was probably a tendency for byssal fixation to be correlated with a very shallow lunule. Thus the specimen from Güngrich shown in Pl. 59, fig. 6, has byssal debris and a much shallower lunule than is usual near Heidelberg (cf. Pl. 59, figs. 1–5) and the same also seems true of the specimens with byssal debris from near Freudenstadt of which Seilacher has published drawings (1954, fig. 7, p. 177). These shallow lunules, which doubtless resulted from the pull of the byssus on the lunular mantle edge, would probably not have provided adequate space for a young *Lima* even if it had succeeded in entering.

Byssal attachment persisted in the Heidelberg–Würzburg area at least up to a length of 30 mm. This is shown by two specimens of this size in the Heidelberg collection from Diedesheim which are pressed lunule downwards against the inner concave side of a large valve of *Lima lineata*. It is at least possible that byssal attachment persisted up to a length of about 55 mm., at which length the first young are found in the lunule (text-fig. 2).

Before leaving this subject, however, it is as well to note that one specimen in the Heidelberg collection from Diedesheim has both a young in the normal position in the lunule and a shell fragment which might represent byssal debris. On the other hand, it is quite possible that the position of this particular fragment is quite accidental.

The southern boundary of the area in which young occur in the lunule is not at present clear. However, single specimens in the Heidelberg collection from Grötzingen and Pforzheim (text-fig. 1) were without young.

Young specimens do not occur in the lunules of *Lima striata* (Schlotheim) in the Heidelberg collection. The lunule of this Upper Muschelkalk species was shallower than is usual in *L. lineata* and this perhaps suggests permanent byssal attachment. The Wellenkalk species *L. radiata* Goldfuss sometimes has young in the same position and orientation as *L. lineata*.

The conclusions of this paper can be summarized as follows:

1. The occurrence of young in the lunules of *Lima lineata* is not accidental since their positions and orientations are almost constant.
2. In life *L. lineata* rested with the lunule on the sea-floor but the lunule was open to the sea by the gap between the umbones. The young could only have entered the lunule with such frequency if they had been photonegative with a tendency to enter crannies.
3. *L. lineata* was not a nest builder since it resembles Recent non-nest-building Limidae, had a fixational byssus, and was usually covered with epizoa which attached during the *Lima*'s lifetime and could not have penetrated a nest of byssal threads.

4. Nevertheless, the nest-building habit could well have evolved from the habit of byssal attachment inside crannies shown by young *L. lineata*, for Limid nests are preferentially made inside cavities.

5. In the Heidelberg area young Limas inside lunules are 10–20 mm. long. A substantial proportion of individuals more than 55 mm. long acted as 'host'. And the young was usually about one-sixth the length of the associated adult.

6. Adult *L. lineata* in south Germany were probably byssally attached. In consequence the lunule was shallow and the gap between the umbones was blocked by byssus and byssal debris so that young could not enter the lunule. Farther north the adults were not byssally attached and so the young could enter.

Acknowledgements. It is a pleasure to thank Dr. and Frau A. Seilacher of Frankfurt University for hospitality and extensive discussion. I should also like to thank Dr. Rösler of Heidelberg for allowing me to examine the collections at that University, Mr. G. F. Elliott for help with the literature, and Dr. R. G. S. Hudson for advice on presentation. The photographs in Pl. 59 are partly the work of Dr. Seilacher and partly of Mr. J. Pope of the Iraq Petroleum Company. Mr. G. Rosser provided advice on statistics.

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R. P. S. JEFFERIES
British Museum (Natural History),
London S.W. 7

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THE CRETACEOUS SPECIES OF *PYRIPORA* D'ORBIGNY AND *RHAMMATOPORA* LANG

by H. DIGHTON THOMAS and G. P. LARWOOD

ABSTRACT. The Cretaceous species of *Pyripora* d'Orbigny and *Rhammatopora* Lang are revised, and *Rhammatopora gasteri* sp.nov. is described.

IN a recent publication (Thomas and Larwood 1956) we have discussed the status of the genera *Pyripora* d'Orbigny and *Rhammatopora* Lang. We have now investigated in greater detail the Cretaceous species of these genera, in the course of which we have examined several hundred zoaria of species of *Pyripora*. This examination has shown, *inter alia*, that *P.* [*Herpetopora*] *anglica* Lang is distinct from *P.* [*H.*] *clavigera* Lang, a junior synonym of *P. laxata* (d'Orbigny), and that the two species may be differentiated on the ratio of the length and width of the aperture.

Most of the zoaria of *Pyripora* which we have examined encrust comparatively smooth substrates. Commonly these are fragments of *Inoceramus* shell (40%), pieces of echinoid test (40%), or fragments of *Ostrea* valve (10%). Less frequently zoaria are also found encrusting belemnite guards (5%) and occasionally the remains of other organisms (5% e.g. brachiopod shell fragments, corals, crinoid plates, and other polyzoa (percentage approximate).

We wish to thank Mr. A. G. Brighton and Mr. R. R. Clarke for the loan of material from the Sedgwick Museum, Cambridge, and the Norwich Castle Museum, respectively; Prof. E. Voigt, of th Geologisches Staatsinstitut, Hamburg, for the loan of German specimens, for information readily given and for permission to reproduce his photograph of the type specimen of *Hippothoa laxata* d'Orbigny and Dr. Anna B. Hastings, of the Zoological Department, British Museum (Nat. Hist.), for discussion on the Recent species of *Pyripora*. Except where otherwise stated, the photographs are by Messrs. M. G. Sawyers and J. V. Brown of the British Museum (Nat. Hist.).

The specimens are referred to by their registered numbers in the various museums: those prefixed by the letter D (e.g. D. 2062) are in the British Museum (Nat. Hist.).

PYRIPORA d'Orbigny

Diagnosis. Zoarium encrusting, uni- or pluri-serial; zooecia pyriform, budded distally and uni- or bi-laterally or both, proximally tapered, often with a very slender tubular proximal cauda; aperture longitudinally oval; cryptocyst usually present forming a proximal shelf or a narrow shelf round most of the opesia; gymnocyst well developed proximally; no calcified basal wall; no ovicells, spines, or avicularia.

Remarks. In all the specimens of the Recent species *Pyripora catenularia* (Fleming), and in all the hundreds of zoaria, and therefore thousands of zooecia of *P. laxata* which we have examined, no ovicells were seen. Hence it is certain that ovicells are not developed in the genus. We therefore exclude from *Pyripora* those species which resemble that genus in other characters but possess ovicells.

We have found that, although the size of zooecia may vary considerably in a given

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zoarium of a species of *Pyripora*, the ratio of the length and width of the aperture varies essentially within narrow limits, and this ratio, in conjunction with the lengths of the zooecia (excluding the caudae), is of great value in recognizing the species.

We reject certain species from *Pyripora* (see p. 381) and include only those given in the following key.

Key to the Cretaceous species of *Pyripora*

1. Majority of caudae narrow and longer than the rest of the zooecia.
   (A) Lc commonly well over 1·00 mm.
      (*a*) ha = 0·25 to 0·43 mm., la = 0·14 to 0·25 mm., apertural ratio 1·40 to 2·35 . . . . *P. laxata* (d'Orbigny)
      (*b*) ha = 0·44 to 0·69 mm., la = 0·17 to 0·27 mm., apertural ratio 2·22 to 3·29 . . . . *P. anglica* (Lang)
   (B) Lc = 0·16 to 0·52 mm., ha = 0·10 to 0·15 mm., la = 0·06 to 0·07 mm. . . . . *P. filum* (Voigt)

2. Majority of caudae broad and shorter than the rest of the zooecia.
   (A) Zoarial budding uni- and bi-lateral occasionally becoming pluriserial; caudae nearly as long as the rest of the zooecia *P. texana* Thomas and Larwood
   (B) Zoarial budding uni- or bi-lateral never becoming pluriserial; caudae distinctly shorter than the rest of the zooecia.
      (*a*) Zoarial budding unilateral; zooecia markedly rounded distally; Lz = 1·20 to 1·50 mm., lz = 0·50 mm.; ha = 0·40 mm.; caudae short, very narrow proximally . . *P. faxensis* (Voigt)
      (*b*) Zoarial budding uni- and probably bi-lateral; zooecia more pointed distally; Lz = 0·50 to 0·75 mm., lz = 0·35 to 0·50 mm.; ha = 0·40 to 0·70 mm.; caudae very short and broad . . . . *P. parvicauda* (Voigt)

3. Caudae absent. Zooecia very small, Lz = 0·30 to 0·35 mm., lz = 0·25 to 0·30 mm.; gymnocyst very narrow . . *P. filimargo* (Voigt)

Pyripora laxata (d'Orbigny)

Plate 60, figs. 1, 2; Plate 61, fig. 2

Hippothoa laxata d'Orbigny 1852, pl. 711, figs. 12–15; 1853, p. 386.
Hippothoa cruciata Reuss 1854, p. 134, pl. 28, fig. 1.
non Hippothoa desiderata Novák 1877, p. 86, pl. 2, figs. 1, 2.
Hippothoa labiata Novák 1877, p. 86, pl. 3, figs. 1–5.
Herpetopora clavigera Lang 1914*a*, p. 6, pl. 2, figs. 4, 5: Voigt 1930, pp. 409, 553, pl. 1, figs. 2. 3; 1949, p. 10, pl. 1, figs. 4–6.
Herpetopora cruciata (Reuss); Lang 1914*a*, pp. 6, 7.
Herpetopora dispersa (von Hagenow); Voigt 1930, pp. 409, 553, pl. 1, fig. 1; [*non Cellepora dispersa* von Hagenow 1839, p. 280; 1846, p. 629, pl. 23*b*, fig. 55].
Herpetopora comptoniensis Brydone 1936, p. 88, pl. 42, fig. 17.
Pyripora cruciata (Reuss); Thomas and Larwood 1956, p. 375 [*partim*].

Lectotype (here chosen). Specimen encrusting an *Echinocorys* test. Senonian, zone of *Belemnitella nucronata*, Meudon, south-west of Paris. D'Orbigny Collection No. 7911, Muséum National d'Hisoire naturelle, Paris.

Diagnosis. *Pyripora* in which the lateral budding is usually bilateral but sometimes nilateral; zooecia inflated, 0·24 to 0·45 mm. wide, with steep lateral walls, distally ounded or slightly tapering, proximally tapered; calcification of frontal membrane and of operculum, and regeneration, relatively common; aperture longitudinally oval ha = 0·25 to 0·43 mm., la = 0·14 to 0·25 mm., apertural ratio = 1·40 to 2·35 bu mostly 1·7 to 1·9; cryptocyst a narrow shelf extending about three-quarters of the way round the opesia; caudae very narrow, tubular, varying greatly in length but usually much longer than the rest of the zooecia, expanding rapidly into the triangular proxima gymnocyst of the zooecium; triangular kenozooecia, with a rounded pore, occasionally occur.

Description. Zoarium encrusting, with distal-median, and usually bilateral, but sometimes unilateral, budding. The distal-median budding is usually single, but very occasionally it may be double. Bilateral budding is more common than unilateral, though both occur at times in the same zoarium. This budding is usually from the distal-latera walls of zooecia and may be at right angles to them or directed distally and obliquely at a lesser angle. In any one series of zooecia unilateral budding may occur on either side Sometimes the budding, whether uni- or bi-lateral, may develop from the caudae.

Caudae slender, tubular and of very variable length—in rare instances absent or very short. The caudae may, however, be several times the length of the rest of the zooecia In any series of zooecia successive caudae are commonly increasingly longer. They are generally straight but may be variously curved. They rapidly expand into the triangular proximal, smooth gymnocyst of the zooecia: the length of the gymnocyst varies, but it is generally well developed.

Zooecia pyriform, longitudinally oval, inflated; lateral and distal walls steep, the latte rounded or slightly pointed distally; calcified basal walls absent in the fossil state. Aperture longitudinally oval, of smaller size but relatively wider than in *Pyripora anglic* (Lang) (cf. text-figs. 1*b–d*). The apertural ratio = 1·40 to 2·35 but is mostly 1·7 t

EXPLANATION OF PLATE 60

Figs. 1, 2. *Pyripora laxata* (d'Orbigny). 1, Type specimen, Mus. nat. Hist. nat. Paris, d'Orbign Collection No. 7911, encrusting test of *Echinocorys*, normal zooecia with, at left, one zooecium wit calcified frontal membrane with central pore, ×20. Photograph by Prof. E. Voigt. 2, Part of th holotype of *Herpetopora clavigera* Lang, Brit. Mus. (Nat. Hist.) 40246, several series of uni- an bi-laterally budded zooecia which have overgrown each other; one zooecium has a calcified fronta membrane and operculum, ×20.

Figs. 3, 4. *Pyripora anglica* (Lang). 3, Paratype, D. 10074, uni- and bi-laterally budded zooecia, one with a calcified frontal membrane and operculum, and one heterozooecium, ×20. 4, Holotype D. 11359, uni- and bi-laterally budded zooecia, some with the frontal membrane and operculum calcified and some regenerated. The linear series of partly developed zooecia is typical of some zoaria, ×20.

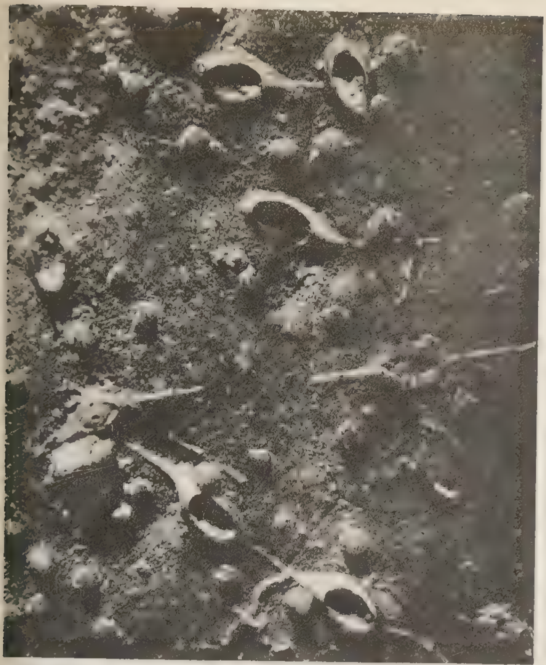
EXPLANATION OF PLATE 61

Fig. 1. *Pyripora anglica* (Lang), paratype, D. 21957. Part of a uni- and bi-laterally budded zoarium showing the tendency for successive zooecia to develop increasingly longer caudae, the occurrence of calcified zooecia in linear series and a triangular heterozooecium, ×20.

Fig. 2. *Pyripora laxata* (d'Orbigny). Holotype of *Herpetopora comptoniensis* Brydone, Sedgwick Museum, B. 36997. Normal zooecia, one with a calcified frontal membrane, ×20.

Figs. 3, 4. *Pyripora filum* (Voigt), Voigt Collection No. 1532. 3, Normal zooecia with thread-like caudae and strongly inflated distal portions encrusting branches of a cyclostomatous polyzoan, ×35. 4, Two smaller normal zooecia of the same specimen with shorter caudae, ×35. Photographs by Department of Photography, University of Durham, King's College, Newcastle upon Tyne.

Fig. 5. *Pyripora texana* Thomas and Larwood, holotype, D. 40541. Uniserially budded normal zooecia in part of the zoarium, ×20.



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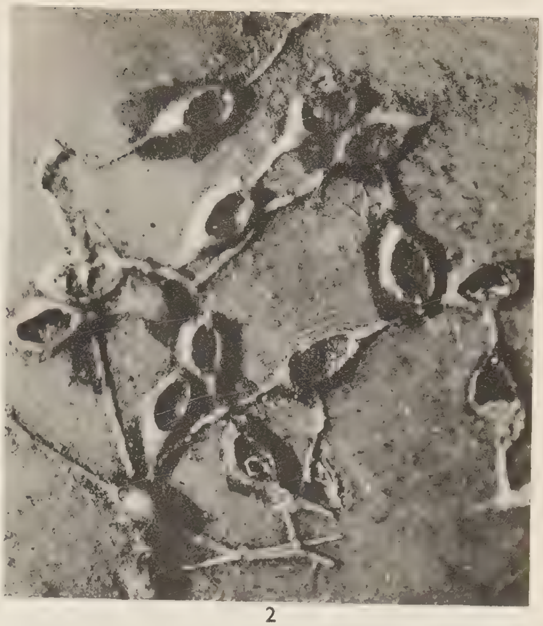

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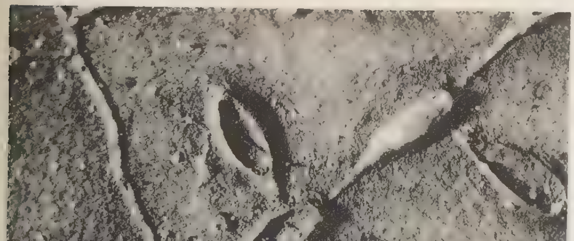

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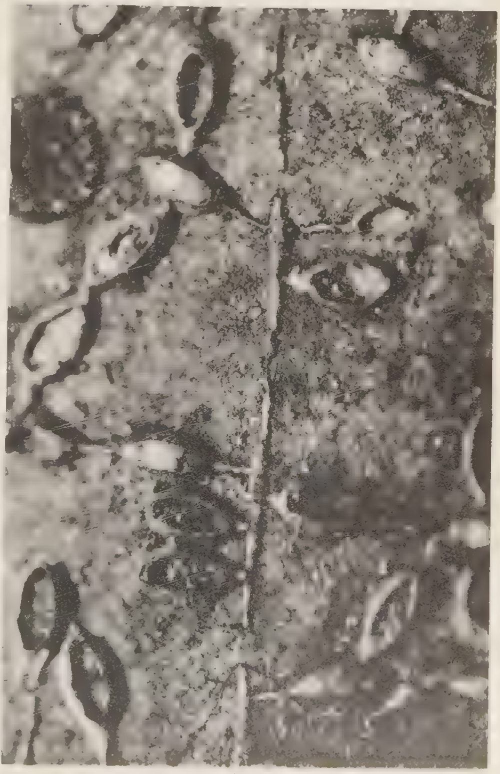

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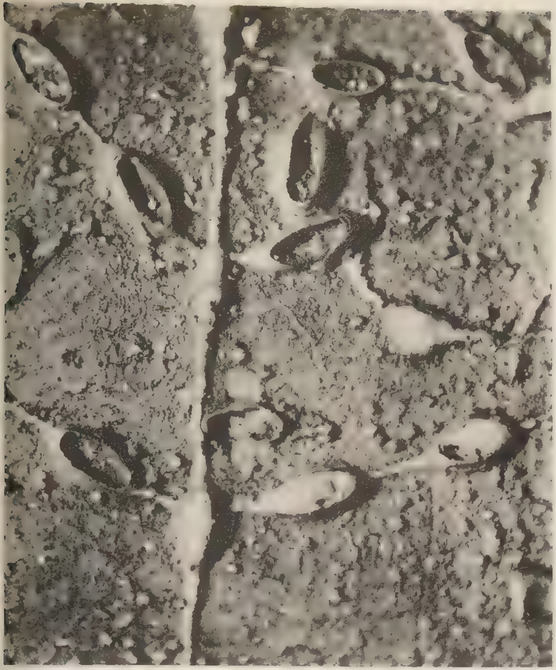

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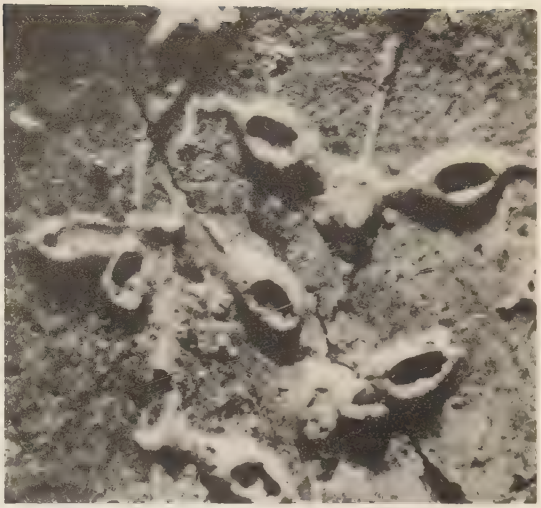

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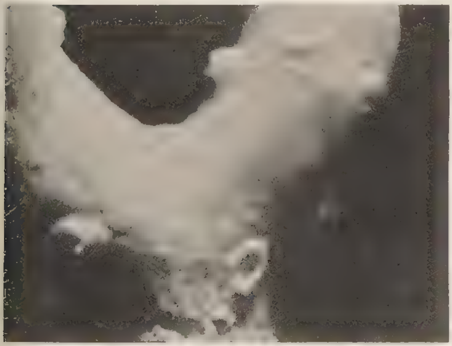

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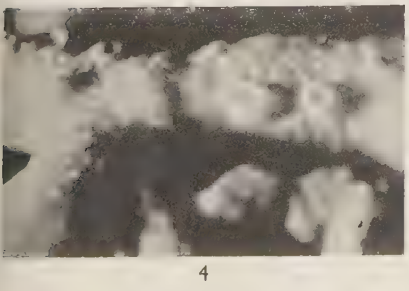

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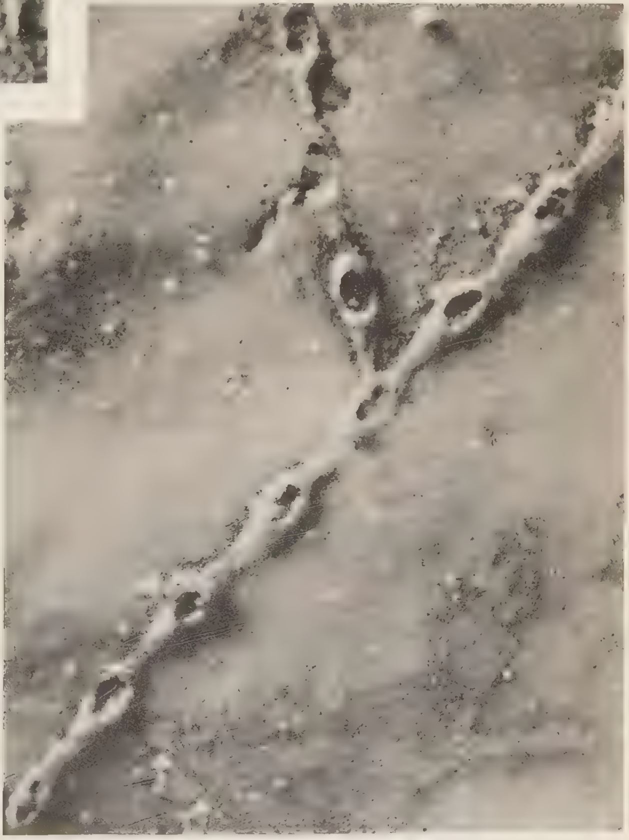


5

1·9. Cryptocyst narrow, slightly descending, extending most of the way round the aperture and producing an oval opesia only slightly smaller than the aperture. Calcification of the frontal membrane and of the operculum is common. It is often complete, but at times incomplete, leaving a small, circular, uncalcified portion near the middle, showing that the calcification has spread from the margin inwards. The calcified opercula are small, straight sided, and evenly rounded distally. Lateral budding frequently, but not always, takes place from zooecia which are thus calcified. Regeneration of zooecia is fairly common and may occur more than once in a given zooecium (text-fig. 1*e*). Sometimes regenerated zooecia have the frontal membrane and operculum completely calcified (text-fig. 1*f–g*).

Kenozooecia are fairly common, and are inflated, triangular, and apparently vicarious: they usually have a rounded, median pore and often bud to give normal zooecia.

Avicularia, spines, and ovicells absent.

Measurements (see text-fig. 1*a*)

Zooecia Lz = 0·66 to 5·18 mm. (or more).
lz = 0·24 to 0·45 mm.
ha = 0·25 to 0·43 mm.
la = 0·14 to 0·25 mm.
ho = 0·23 to 0·41 mm.
lo = 0·13 to 0·14 mm.
Lc = up to 4·00 mm. (or more).
lc = about 0·07 mm. (unless absent).

Apertural ratio = 1·40 to 2·35, but mostly 1·7 to 1·9.

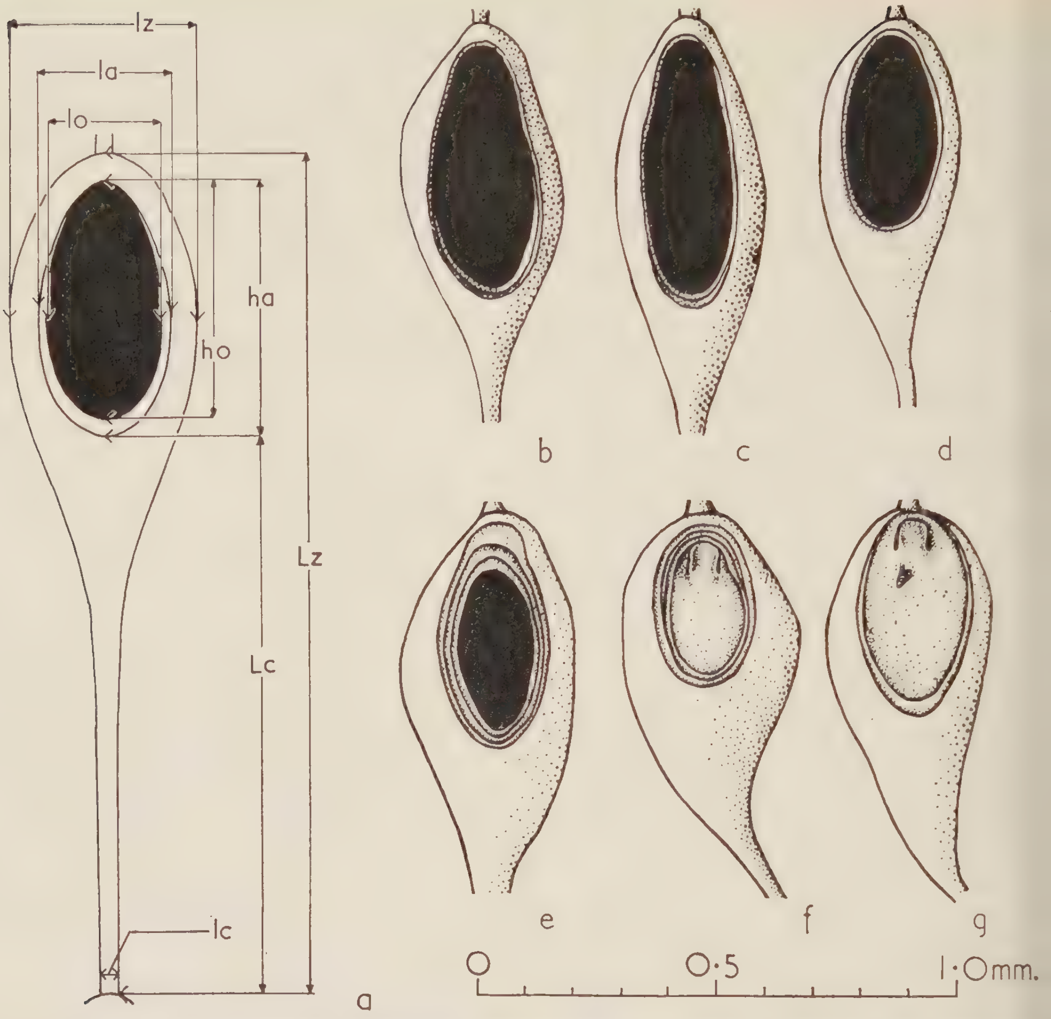
Measurements of a large number of zooecia have been made on specimens ranging rom the Cenomanian to the Danian. Lz is widely variable, for it includes measurement of the cauda as well as the rest of the zooecium; lz, ha, la, ho, and lo are less variable than Lz or the caudal measurements (Lc, lc), and are consequently of greater diagnostic value. Lc is extremely variable; caudae may be lacking, or they may be up to three or four or more times as long as the rest of the zooecia; the caudae are, however, always very narrow.

Remarks. This revision shows that wide variation may occur not only between zoaria but also within the zoaria themselves.

In 1839 von Hagenow briefly described (p. 280) a polyzoan from Rügen as *Cellepora dispersa*: unfortunately he gave no figure. Subsequently (1846, p. 629, pl. 23*b*, fig. 55), he gave a more detailed description of the species, accompanied by a figure, on which the nterpretation of *Cellepora dispersa* must be based. In the upper right-hand part of the igure he showed three circular heterozooecia which can be matched in a species from Rügen which Lang (1914*b*, p. 439, pl. 34, fig. 3) described as *Marssonopora dispersa* (von Hagenow). We agree with Lang's interpretation. Thus, in contrast to Voigt's opinion 1930, p. 409) von Hagenow's specific name *dispersa* is not available for the Chalk pecies lacking avicularia.

Lang (1914*a*, p. 7) considered *Hippothoa gracilis* d'Orbigny (1852, pl. 711, figs. 12–15; 853, p. 386) to be a species of his genus *Herpetopora*, but the nature of its orifice and he occurrence of ovicells show clearly that it does not belong to that genus, and, thereore, not to *Pyripora*.

Prof. E. Voigt has recently sent us photographs of the type specimen of *Hippothoa axata* d'Orbigny (1852, pl. 711, figs. 12–15; 1853, p. 386), d'Orbigny Collection No. 7911. rom these it is clear that the species is the same as *Herpetopora clavigera* Lang of which



TEXT-FIG. 1. *a*, Measurements: Lz = length of zooecium; lz = width of zooecium; ha = length o aperture; la = width of aperture; ho = length of opesia; lo = width of opesia; Lc = length of cauda lc = width of cauda. *b*, *c*, Distal ends of two normal zooecia of *Pyripora anglica* (Lang): (*b* and *c* from D. 40489). *d–g*, Distal ends of zooecia of *P. laxata* (d'Orbigny): (*d*—D. 40135, normal zooecium *e*—D. 40158, repeatedly regenerated; *f*—D. 40364, repeatedly regenerated with completely calcified frontal membrane and operculum; *g*—D. 40140, regenerated with completely calcified frontal membrane and operculum).

we have much well-preserved material. *Hippothoa laxata* d'Orbigny therefore becomes the first available name for the species dealt with here.

Hippothoa desiderata Novák (1877, p. 10, pl. 2, figs. 1, 2) was placed by Lang (1914*a*, p. 7) in *Herpetopora*, but *Hippothoa desiderata* was described by Novák as possessing small, hemispherical ovicells. The species is thus excluded from *Pyripora*.

Among the large number of specimens from the English, and some foreign, Chalk which we have examined there are variations in the branching and in the caudal and other zooecial characters which show that *Hippothoa laxata* d'Orbigny (1852; 1853), *H. cruciata* Reuss (1854), *H. labiata* Novák (1877), *H. dispersa* Marsson (1877) *non* von Hagenow, *Herpetopora clavigera* Lang (1914*a*) and *H. comptoniensis* Brydone (1936) are all synonymous.

The species is widely distributed in Europe—see the localities to which the references in the synonymy apply. Prof. E. Voigt has recently sent us a photograph of a specimen encrusting a *Gryphaea* from the Maastrichtian of Burunduk Kaja, Crimea (Coll. Inst. Hist. Geol. Fac. Geol. Moscow, No. 8084–5/*b*), which he had received from Prof. Najdin of Moscow. He has also told us of a specimen he had found on an *Echinocorys* from the Upper Maastrichtian of Hallembaye, near Haccourt, north-east of Liège, Belgium.

Stratigraphical distribution. Cenomanian, zone of *Schloenbachia varians*, to Danian (see remarks on *Pyripora anglica*).

Specimens. A. British. From numerous localities in south-east and east England, ranging from Dorset and the Isle of Wight to Lincolnshire. (1) British Museum (Natural History): (*a*) Zone of *Belemnitella mucronata*—43 specimens including 40246, D. 3243, D. 20607–8, D. 28898, D. 40135, and D. 40140. (*b*) Zone of *Gonioteuthis* [*Actinocamax*] *quadrata*—169 specimens including D. 2647, D. 3244, D. 20610, D. 28081–100, D. 28795, D. 29054, D. 29063, D. 40158, and D. 40364. (*c*) Zone of *Offaster pilula*—D. 28917, D. 29842–5, D. 40532–3. (*d*) Horizon and locality unknown—D. 35352. (2) Norwich Castle Museum: Zone of *B. mucronata*—N.C.M. 76.937(34–39). (3) Sedgwick Museum: (*a*) Zone of *Ostrea lunata*—B. 60756–60, B. 61001–2, B. 80750-60. (*b*) Zone of *B. mucronata*—B. 80676, B. 80691–749. (*c*) Zone of *G.* [*A.*] *quadrata*—B. 80675, B. 80677–88. (*d*) Zone of *B. mucronata* or *G.* [*A.*] *quadrata*—B. 80689–90. (*e*) Zone of *O. pilula*—B. 80674. (*f*) Zone of *Schloenbachia varians*—B. 36997, type specimen of *Herpetopora comptoniensis* Brydone.

B. Danish. Danian. Faxe, Seeland—?D. 9113, ?D. 29014, ?D. 40537–8.

C. German specimens lent by Prof. E. Voigt, Geologisches Staatsinstitut, Hamburg. (*a*) Upper Maastrichtian, Hemmoor, Coll. Voigt 3171, 3173. (*b*) Lower Maastrichtian, Hemmoor, Coll. Voigt 3166; Luneburg (Zeltburg), Coll. Voigt 3167, 3168; and Rügen, Coll. Voigt 3163–5. (*c*) Maastrichtian, division unspecified, Hemmoor, Coll. Voigt 3172. (*d*) Zone of *B. mucronata* or *G.* [*A.*] *quadrata*, Grube Alsen, near Lägerdorf, Coll. Voigt 3169. (*e*) Zone of *G.* [*A.*] *quadrata*, Lägerdorf, Coll. Voigt 3170.

Pyripora anglica (Lang)

Plate 60, figs. 3, 4; Plate 61, fig. 1

Herpetopora anglica Lang 1914*a*, pp. 6, 7, pl. 2, figs. 1–3; 1914*b*, p. 436; 1921, p. 83; 1925, p. 229, pl. 20, fig. 7, pl. 21, fig. 18: Canu and Bassler 1920, p. 81, text-fig. 22; 1923, p. 18, text-fig. 1c; Bassler 1935, p. 124; 1953, p. G157, text-fig. 119, 8.

Pyripora cruciata (Reuss) Thomas and Larwood 1956, p. 370 [*partim*].

Holotype. D. 11359. Specimen encrusting large fragment of *Volvinoceramus involutus*. Senonian, base of zone of *Micraster coranguinum* or top of zone of *M. cortestudinarium*, Chatham, Kent; W. Gamble Collection.

Diagnosis. Pyripora like *P. laxata* (d'Orbigny) but ha = 0·44 to 0·69 mm., la = 0·17 to ·27 mm., apertural ratio = 2·22 to 3·29, but mostly about 2·5.

Measurements

Zooecia Lz = 0·69 to 4·89 mm. (or more).
lz = 0·25 to 0·47 mm.
ha = 0·44 to 0·69 mm.
la = 0·17 to 0·27 mm.
ho = 0·42 to 0·67 mm.
lo = 0·16 to 0·26 mm.
lc = 0 to 3·87 mm. (or more).
lc = about 0·08 mm., unless absent.

Apertural ratio = 2·22 to 3·29 (mostly about 2·5).

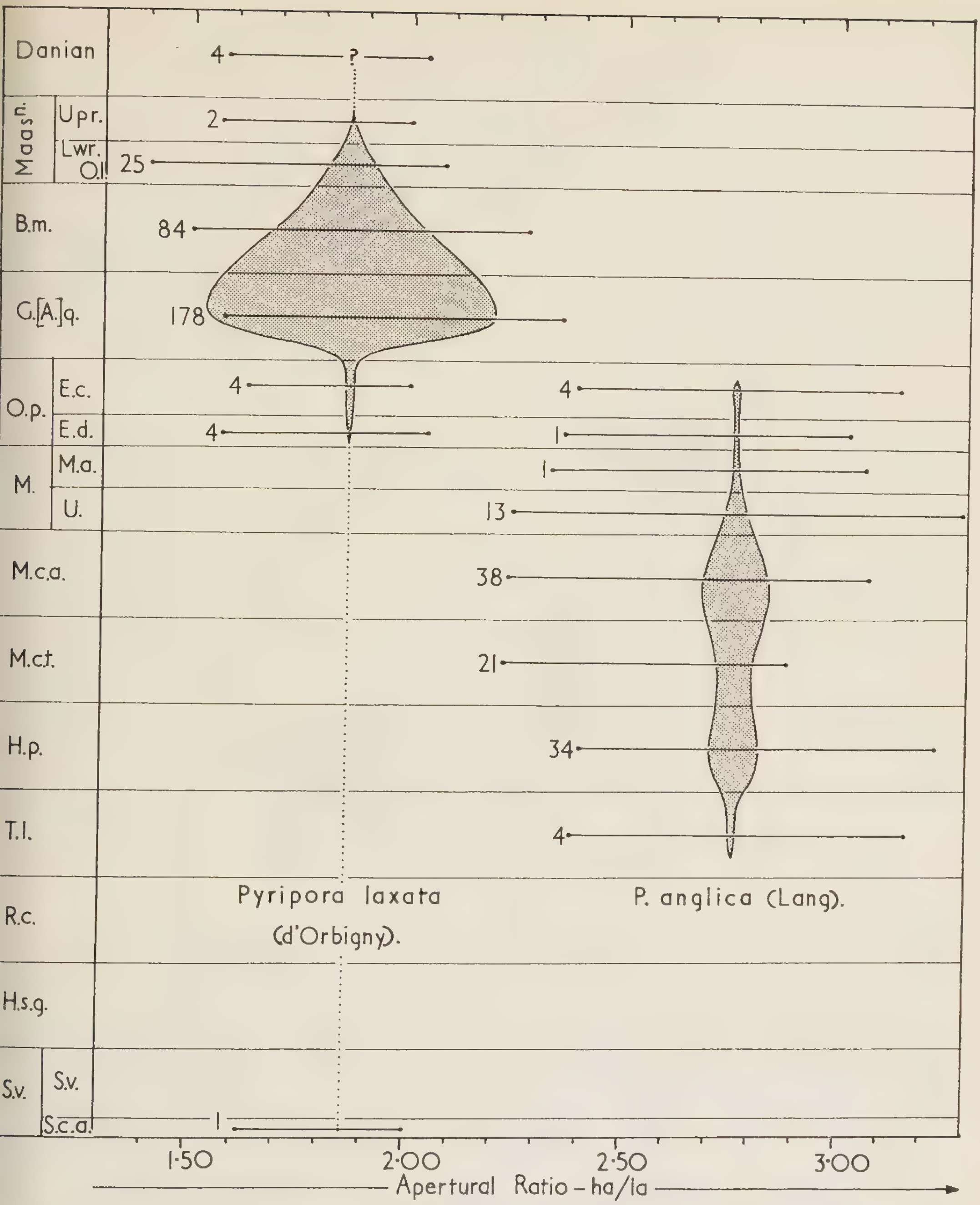
Remarks. P. anglica (Lang) very closely resembles *P. laxata* (d'Orbigny) in its zoarial and zooecial characters. The mode of budding of the zoarium is the same; caudae are of the same narrow type though apparently very slightly wider, frequently of increasing length in a given single series; but the zooecia, excluding the caudae, are usually longer. The aperture is larger and distinctly longer and narrower than in *P. laxata* (cf. text-figs. 1*b–d*), and the gymnocyst proportionately smaller. Other characters, such as the presence of a narrow, proximal cryptocyst, the occurrence of series of sealed zooecia, and the presence of regenerated zooecia and triangular kenozooecia are the same.

Lang (1914*a*) diagnosed *Herpetopora anglica* as having 'zooecia that taper somewhat distally as well as proximally; with regularly elliptical termens [apertural margins]'. As distinct from this, he defined *H. clavigera* as a '*Herpetopora* with zooecia hardly tapering distally and consequently more or less pear-shaped, having their outlines bounded by steeply curved sides . . .'. These distinctions in the general shape of the zooecia of *H. anglica* and *H. clavigera* are not clear either in the new material which we have examined or in Lang's original specimens. In his key to the genus *Herpetopora* (1914*a*, p. 7) Lang has described the termen [apertural margin] as 'elliptical rather than oval' in *H. anglica*; in other words the aperture is longer and narrower in this species, the apertural ratio being about 2·5. This and the somewhat larger zooecia are the only significantly constant differences from *H. clavigera* Lang, and are clearly confirmed here by many measurements on abundant material of both species.

P. anglica (Lang) is less common than *P. laxata* (d'Orbigny) and has a more restricted stratigraphical range in the English Chalk. Lang (1913, p. 172) has referred to *Herpeto-pora clavigera* [= *Pyripora laxata* (d'Orbigny)] and to *Herpetopora anglica* [= *Pyripor* *anglica* (Lang)] as species which 'divide the English Chalk between them at the junctio of the *quadratus* and *Marsupites* zones'. Our examination of these species supports Lang statement but has shown that *Pyripora laxata* (d'Orbigny) first occurs in the Cenomania where it is represented by one well-preserved zoarium, Sedgwick Museum, B. 3699 (the type specimen of *Herpetopora comptoniensis* Brydone). The species next occurs in the zone of *Offaster pilula* and becomes very abundant in the succeeding zones, possibl surviving into the Danian from which we have seen four rather poorly preserved specimens. In contrast, *Pyripora anglica* (Lang) first occurs in the zone of *Terebratulina lata* and becomes more abundant in the zones of *Holaster planus*, *Micraster cortestudinarium*, and *M. coranguinum*, and survives, much reduced in numbers, into the upper part of the zone of *Offaster pilula* (see text-fig. 2).

Stratigraphical distribution. Turonian, zone of *Terebratulina lata*, to Senonian, zone of *Offaster pilula.*

Specimens. From numerous localities in south-east and east England. (1) British Museum (Natural History): (*a*) Zone of *Offaster pilula*—D. 28239, D. 29846, D. 40529–31. (*b*) Zone of *Marsupites testudinarius*—D. 29847, D. 40526–8. (*c*) Zone of *Micraster coranguinum*—D. 4189, D. 8213, D. 10074, D. 11126, D. 21218, D. 21955–8, D. 24361–2, D. 28240–1, D. 28899–900, D. 29098, D. 31825, and 22 other specimens. (*d*) Zone of *M. cortestudinarium*—D. 8214, D. 11359, D. 21949–51, D. 28242–3, D. 29847, D. 40504–12. (*e*) Zone of *M. coranguinum* or *M. cortestudinarium*—D. 11372. (*f*) Zone of *Holaster planus*—D. 8387, D. 21219, D. 29848, D. 40489, and 30 other specimens. (*g*) Zone of *Terebratulina lata*—D. 20611, D. 40332–4. (*h*) Horizon and locality unknown—D. 38849. (2) Sedgwick Museum: (*a*) Zone of *Marsupites testudinarius*—B. 80662–7, B. 80670–3. (*b*) Zone of *Micraster cortestudinarium*—B. 80655–60.



EXT-FIG. 2. Stratigraphical distribution of *Pyripora laxata* (d'Orbigny) and *P. anglica* (Lang). The ange in value of apertural ratios is shown for 415 specimens from the Chalk. The figures to the left f each line indicate the number of measurable specimens available to us from each zone. (Maasn.—aastrichtian; O.l.—zone of *Ostrea lunata*; B.m.—zone of *Belemnitella mucronata*; G.[A.]q.—zone of *onioteuthis* [*Actinocamax*] *quadrata*; O.p.—zone of *Offaster pilula*; E.c.—subzone of *Echinocorys cutata* var. *cincta*; E.d.—subzone of *E. scutata* var. *depressula*; M.—zone of *Marsupites testudinarius*; .a.—subzone of *M. testudinarius*; U.—subzone of *Uintacrinus westfalicus*; M.c.a.—zone of *Micraster oranguinum*; M.c.t.—zone of *M. cortestudinarium*; H.p.—zone of *Holaster planus*; T.l.—zone of *erebratulina lata*; R.c.—zone of *Orbirhynchia* [*Rhynchonella*] *cuvieri*; H.s.g.—zone of *Holaster sub-lobosus*; S.v.—zone and subzone of *Schloenbachia varians*; S.c. a.—subzone of *Stauronema carteri*).

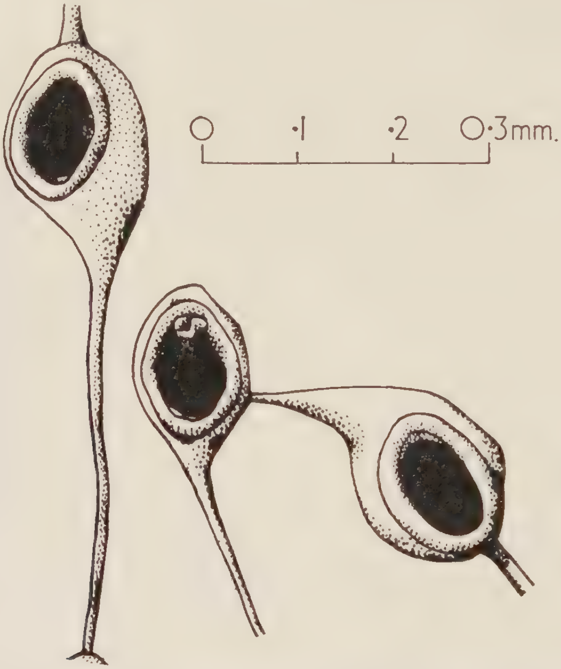
Pyripora filum (Voigt)

Plate 61, figs. 3, 4

Herpetopora filum Voigt 1930, pp. 410, 553, pl. 1, figs. 8–10.
?*non Herpetopora filum* Voigt; Balavoine 1956, p. 157, pl. 6, fig. 2.

Type specimen. That figured by Voigt 1930, pl. 1, fig. 10. Maastrichtian. Maastricht.

Diagnosis. Pyripora with small, strongly inflated zooecia; apertural rim thick and prominent; ha = 0·10 to 0·15 mm., la = 0·06 to 0·07 mm.; small proximal cryptocyst present; Lc = 0·16 to 0·52 mm., lc = 0·02 to 0·155 mm.



TEXT-FIG. 3. Three normal zooecia of *Pyripora filum* (Voigt). E. Voigt Collection 1532. Upper Maastrichtian, Maastricht.

Description. Zoarium encrusting, with single distal-median and uni- and bi-lateral budding. Bilateral budding is apparently more common than unilateral, but both may occur in the same zoarium (e.g. Voigt 1930, pl. 1, fig. 9 and Voigt Collection 1532). Lateral budding is commonly from the distal-lateral walls of zooecia and is directed distally and obliquely.

Caudae straight, or only slightly irregular, tubular, very narrow, of variable length with a maximum of 1·00 mm. (see Voigt, 1930, p. 410) but usually much shorter. A cauda may be twice as long as the rest of the zooecium. The caudae expand abruptly into a proximal, triangular, smooth gymnocyst which is nearly as long as the aperture and which rises steeply to the apertural rim and extends, much narrowed, round the aperture.

Zooecia longitudinally oval, strongly inflated; lateral and distal walls fairly steep.

Aperture longitudinally oval, small, with a prominent wide rim. Cryptocyst a slight, crescentic, sloping shelf within the proximal margin of the aperture. Opesium only slightly smaller than the aperture. Calcification of the frontal membrane may be complete (e.g. Voigt, 1930, pl. 1, fig. 9); calcification of the operculum and regeneration of the zooecia have not been seen.

Kenozooecia not seen.

Spines, avicularia, and ovicells absent.

Measurements

Zooecia Lz = 0·28 to 0·65 mm.
lz = 0·12 to 0·15 mm.
ha = 0·10 to 0·15 mm.
la = 0·06 to 0·07 mm.
ho = 0·09 mm.
lo = 0·06 mm.
Lc = 0·16 to 0·52 mm. (occasionally up to 1·00 mm.).
lc = 0·02 to 0·155 mm.

Apertural ratio = 1·66.

Remarks. *P. filum* (Voigt) is distinguished from other caudate Cretaceous *Pyripora* species by its unusually small size, its prominent, wide apertural rim, and its straight, narrow caudae (see text-fig. 3).

The type specimen from Maastricht is, according to Voigt's description, more robust than the material which he has seen from the *Gonioteuthis* [*Actinocamax*] *mammillata* Chalk of Ifö, Sweden. Balavoine (1956, p. 157, pl. 6, fig. 2) has described, as *Herpetopora filum* Voigt, a specimen from limestones containing *Hercoglossa danica* at Vigny, Seine-et-Oise, France. Its very small size (Lz = 0·12 to 0·15 mm., lz = 0·05 to 0·06 mm.) distinguishes it from *P. filum* (Voigt) as described above.

Stratigraphical distribution. Senonian, *G.* [*A.*] *mammillata* Chalk (upper part of zone of *G.* [*A.*] *quadrata*) and Upper Maastrichtian.

Specimen. Part of a zoarium encrusting a ramose cyclostomatous polyzoan; Upper Maastrichtian, 'Nd Geul-Tal b. Berg b. Maastricht'; E. Voigt Collection 1532.

Pyripora texana Thomas and Larwood

Plate 61, fig. 5

Pyripora texana Thomas and Larwood 1956, pp. 371, 372, text-figs. 2, 3.

Diagnosis. *Pyripora* with somewhat irregular uni- or bi-lateral budding, sometimes becoming pluriserial; Lz = 0·72 to 0·93 mm., lz = 0·21 to 0·33 mm.; ha = 0·33 to 0·36 mm., la = 0·15 to 0·21 mm.; caudae relatively broad, about as long as the rest of the zooecia, Lc = 0·30 to 0·50 mm., lc = 0·07 to 0·10 mm.

Remarks. This earliest known species of *Pyripora* has been described recently by the present authors.

Pyripora faxensis (Voigt)

Herpetopora faxensis Voigt 1930, pp. 410, 553, pl. 1, fig. 4.

Type specimen. That figured by Voigt 1930, pl. 1, fig. 4. Danian. Faxe, Seeland, Denmark.

Diagnosis (based on Voigt's 1930 description and figure). *Pyripora* with zooecia inflated, well rounded distally, tapered proximally, Lz = 1·20 to 1·50 mm., lz = 0·50 mm.;

aperture oval, not much longer than wide, ha = 0·40 mm.; proximal cryptocyst apparently present; caudae short, tubular, rapidly widening distally into a long, wide, triangular, proximal gymnocyst.

Measurements (according to Voigt 1930, p. 410)

Zooecia	Lz = 1·20 to 1·50 mm.	ha = 0·40 mm.
	lz = 0·50 mm.	(no other measurements recorded)

Remarks. Voigt (1930, p. 410) has suggested, 'Apparently this [*P. faxensis*] is the largest species of the *dispersa* group—and is thereby distinguished from the other species' [translation]. Voigt's term '*dispersa* group' implies all the Cretaceous species of *Pyripora*, other than *P. texana*, which possess caudae. In addition to the generally greater size of zooecia in *P. faxensis*, their marked distal rounding, the oval aperture, which is almost as wide as long, the short, straight caudae, and the long, wide, triangular, proximal gymnocyst also appear to be of diagnostic value. There are no specimens in the collections examined.

Stratigraphical distribution. Danian.

Pyripora parvicauda (Voigt)

Herpetopora parvicauda Voigt 1930, pp. 411, 553, pl. 1, fig. 11.

Type specimen. That figured by Voigt 1930, pl. 1, fig. 11. 'Oberer Emscher.' Lengede-Broistedt, Gr. Ilsede.

Diagnosis (based on Voigt's 1930 description and figure). *Pyripora* with zooecia distally pointed; Lz = 0·50 to 0·75 mm., lz = 0·35 to 0·50 mm.; caudae very short and broad; la = 0·40 to 0·70 mm.; cryptocyst apparently present; gymnocyst narrow distally and laterally, wider and somewhat triangular proximally.

Measurements (according to Voigt 1930, p. 411)

Zooecia	Lz = 0·50 to 0·75 mm.	ha = 0·40 to 0·70 mm.
	lz = 0·35 to 0·50 mm.	(no other measurements recorded).

Remarks. *Pyripora parvicauda* is distinguished particularly by its 'very short caudal part' which is 'hardly developed' (Voigt, 1930, p. 411, translation). The distally pointed zooecial outline is also distinctive. There are no specimens in the collections examined.

Stratigraphical distribution. Senonian, upper part of the Emscherian (? zone of *Micraster coranguinum* or zone of *Marsupites testudinarius*).

Pyripora filimargo (Voigt)

Herpetopora filimargo Voigt 1930, pp. 411, 553, pl. 1, fig. 12.

Type specimen. That figured by Voigt 1930, pl. 1, fig. 12. 'Mammillatensenon' (upper part of zone of *Gonioteuthis* [*Actinocamax*] *quadrata*). Ifö, Sweden.

Diagnosis (based on Voigt's 1930 description and figure). *Pyripora* with zooecia in which Lz = 0·30 to 0·35 mm., lz = 0·25 to 0·30 mm.; caudae absent; cryptocyst apparently absent; gymnocyst very narrow.

Measurements (according to Voigt 1930, p. 411)

Zooecia Lz = 0·30 to 0·35 mm. lz = 0·25 to 0·30 mm.
(no other measurements recorded)

Remarks. The absence of caudae is particularly distinctive in this species, and, as Voigt (1930, p. 411) has stated, the zooecia are very small with an 'exceptionally narrow border [gymnocyst]' (translation). There are no specimens in the collections examined.

Stratigraphical distribution. 'Mammillatensenon' (upper part of zone of *Gonioteuthis* [*A*]. *quadrata*).

Species previously assigned to *Herpetopora* (= *Pyripora*) but here excluded from *Pyripora*

1. *Herpetopora danica* Lang (1914*a*, p. 7, pl. 2, figs. 6, 7). Prof. E. Voigt has very kindly lent us a well-preserved specimen, E. Voigt Coll. 3174, from the Upper Maastrichtian of Hemmoor, encrusting a piece of echinoid test. This specimen is like the holotype in its fundamental features, but at least three zooecia have prominent hyperstomial ovicells. It is clear that although ovicells occur they are not frequent and that in less extensive zoaria they may not therefore be present—as is the case in the holotype of *Herpetopora danica* Lang (D. 19429) and in the paratype (D. 44407). However, as all other zoarial and zooecial characters are so similar, the species as a whole may be regarded as ovicelled and therefore excluded from *Pyripora*. We would refer it provisionally to *Membranipora* s.l.
2. *Herpetopora danica* Lang subsp. *titania* Voigt (1949, p. 9, pl. 1, figs. 1–3). We agree that this subspecies, the type of which has been lent to us by Prof. Voigt (E. Voigt Coll., 135), belongs to *Herpetopora danica*. As it belongs to an ovicelled species it also is excluded from *Pyripora*.

RHAMMATOPORA Lang

?*Crisia* Mantell 1844, p. 285; 1854, p. 269.
?*Hippothoa* Morris 1854, p. 125 [*partim*].
Membranipora Vine 1890, p. 484 [*partim*]; 1891*a*, p. 385 [*partim*]; ? 1891*b*, p. 395; 1892, p. 154; 1893, p. 335 [*partim*].
Rhammatopora Lang 1915, p. 496 [*partim—Crisia johnstoniana* Mantell *excl.*]; Canu, 1916, p. 58; Thomas and Larwood 1956, p. 372.
Pyripora: Bassler, 1935, pp. 23, 181 [*partim*]; 1953, p. G158 [*partim*].

Type species (by original designation). *Membranipora gaultina* Vine 1890, p. 484, pl. 19, figs. 13*a–d*, Gault. Cambridge.

Diagnosis. Zoarium encrusting, uniserial; zooecia pyriform, budded distally and uni- or bi-laterally or both, proximally tapered, with slender, tubular, proximal caudae; aperture longitudinally oval; cryptocyst forming a narrow descending shelf, particularly on the proximal side of the opesia; gymnocyst well developed proximally; differs from *Pyripora* in having an apertural rim slightly raised with numerous small apertural spine-bases; no calcified basal wall; no avicularia or ovicells.

Remarks. We have already indicated elsewhere (Thomas and Larwood, 1956, p. 372) that the 'rhamma', described by Lang (1915, p. 497) as a feature of generic importance, is of no systematic significance: it is an irregular crack developed along the caudae during fossilization. However, *Rhammatopora* Lang may be distinguished from *Pyripora* d'Orbigny by its numerous small apertural spine-bases. We thus differ from Canu (1916, p. 59) and from Bassler (1935, pp. 23, 181; 1953, p. G158) who regarded the two genera as synonymous.

Charixa vennensis Lang, the type species of *Charixa* Lang (1915, p. 500), is a multi-serial species which becomes uni-serial in places (op. cit., pl. 17, fig. 5). In other respects, e.g. the presence of apertural spine-bases, it resembles *Rhammatopora*, and it seems to bear a similar relationship to *R. gaultina* as *Pyripora pyriformis* (Michelin) does to *P. laxata* (d'Orbigny)—see Thomas and Larwood (1956, p. 370). But more material is needed to elucidate further the structure of *Charixa*.

Distelopora Lang (1915, p. 502) differs from *Rhammatopora* in possessing a very wide, distinctive cryptocyst, which contrasts with the slight, narrow, proximal cryptocyst of *Rhammatopora*.

Lang (1915, p. 498) regarded *Crisia johnstoniana* Mantell as a species of *Rhammatopora*. As he pointed out, only Mantell's figures are available for the interpretation of the species. They are much stylized, the dimensions of the specimens are not recorded, and there is confusion as to the true locality of the material. *Crisia johnstoniana* Mantell was recorded by Mantell (1844, p. 285; 1854, p. 269) from the Lower Greensand of Maidstone, Kent, and possibly from the Shanklin Sands of the Isle of Wight. The systematic position of *Crisia johnstoniana* is quite uncertain, and we doubt whether it can be referred to *Rhammatopora*.

Stratigraphical distribution. Albian to Cenomanian, upper part of zone of *Schloenbachia varians*.

Key to the species of *Rhammatopora*

1. Aperture up to 0·45 mm. long and up to 0·25 mm. wide; number of apertural spine-bases 15–20 (commonly 18) . . . . 1. *R. gaultina* (Vine)
2. Aperture up to 0·27 mm. long and up to 0·17 mm. wide; number of apertural spine-bases apparently 10–13 (commonly 12) . . . . . 2. *R. gasteri* sp. nov.

Rhammatopora gaultina (Vine)

Plate 62, figs. 1, 2

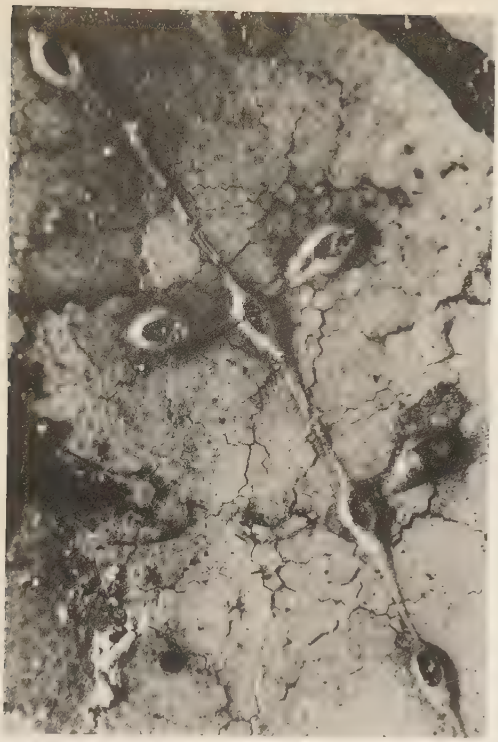
Membranipora gaultina Vine 1890, pp. 461, 484, pl. 19, fig. 13*a–d*; 1891*a*, pp. 385, 396; 1892, pp. 154, 155, pl. 6, fig. 15; 1893, p. 335.
Membranipora gaultina var. Vine 1891*b*, p. 395.
Rhammatopora gaultina (Vine); Lang 1915, pp. 498, 499, pl. 17, fig. 2.
Rhammatopora pembrokiae Lang 1915, pp. 498, 499, pl. 17, figs. 3, 4.
Rhammatopora vinei Lang 1915, p. 498, pl. 17, fig. 1.
Pyripora gaultina (Vine); Bassler, 1935, p. 189.

EXPLANATION OF PLATE 62

Figs. 1, 2. *Rhammatopora gaultina* (Vine). 1, Holotype of *Rhammatopora pembrokiae* Lang, D. 22987, uni- and bi-laterally budded normal zooecia with minute apertural spine-bases, ×20. 2, Holotype of *Rhammatopora gaultina* (Vine), D. 2062, normal zooecia with minute apertural spine-bases, ×20.

Figs. 3, 4. *Rhammatopora gasteri* sp. nov. Holotype, D. 40472. 3, Part of zoarium with normal zooecia with minute apertural spine-bases, ×35. 4, Detail of two zooecia and part of a damaged third zooecium, the most distal zooecium with two very distinct spine-bases on the distal part of the apertural rim, ×75. Photographs by Dept. of Photography, University of Durham, King's College, Newcastle upon Tyne.

PLATE 62



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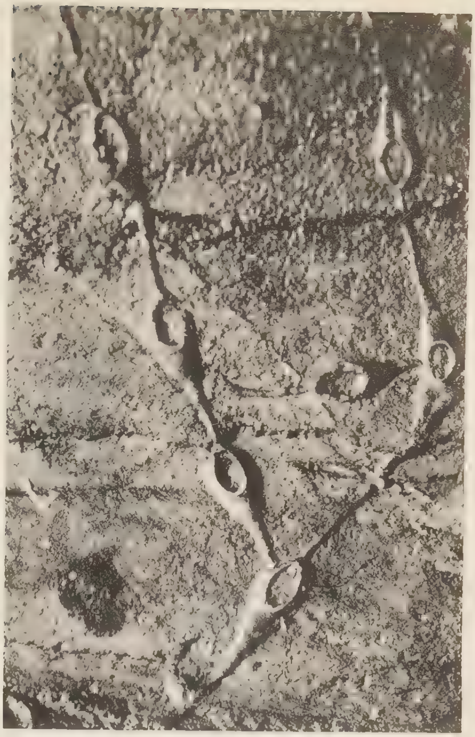

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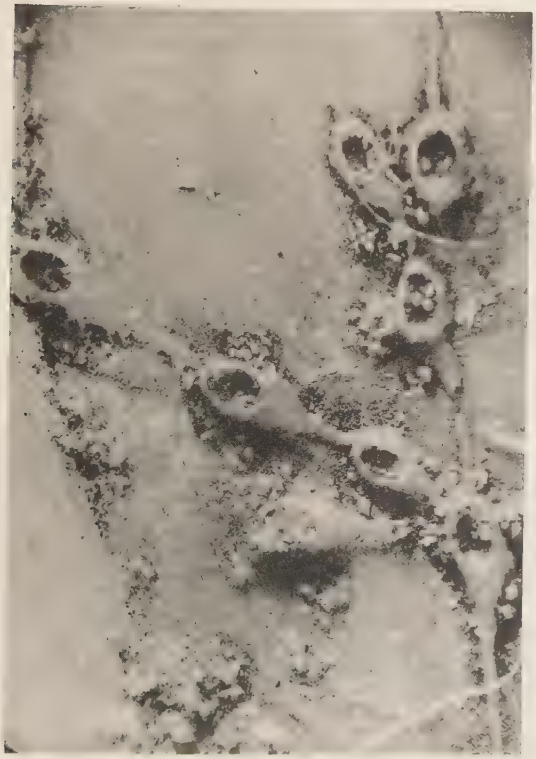

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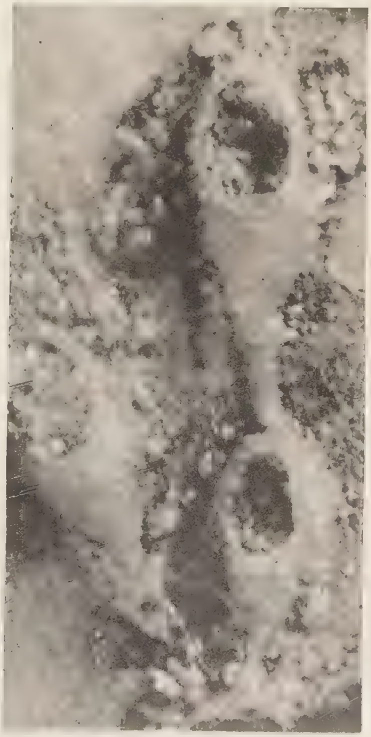


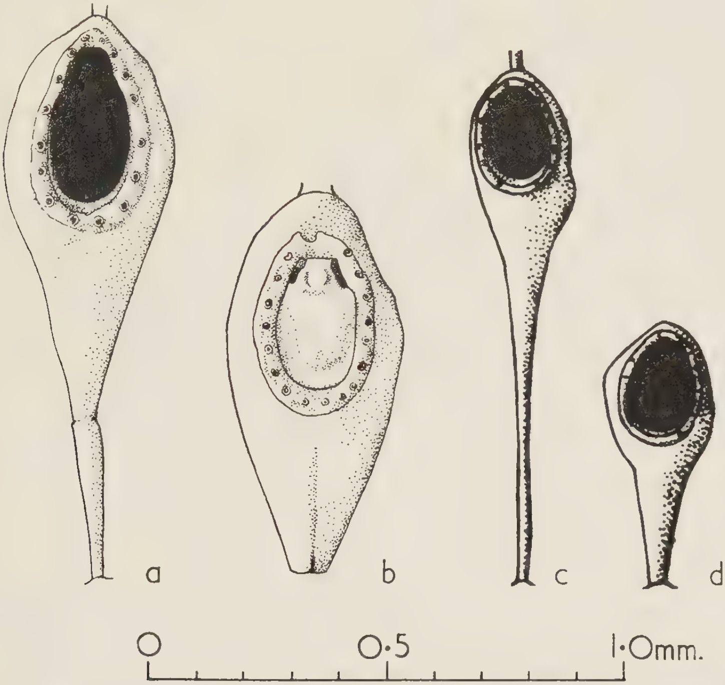
4

THOMAS and LARWOOD, *Rhammatopora*

Lectotype (chosen Lang 1915, p. 499). D.2062. Incomplete zoarium encrusting a fragment of *Inoceramus*. Albian, Gault. Cambridge. T. Jesson Collection.

Diagnosis. Rhammatopora with aperture 0·27 to 0·45 mm. long, 0·16 to 0·25 mm. wide; opesia 0·22 to 0·38 mm. long, 0·15 to 0·17 mm. wide; 15 to 20, commonly 18, apertural spine-bases.

Description. Zoarium encrusting; budding distal-median and, in places, uni- and bilateral almost at right angles.



TEXT-FIG. 4. *a*, *b*, *Rhammatopora gaultina* (Vine). *a*—D. 2062, lectotype, a normal zooecium; *b*—D. 22905, paratype of *R. pembrokiae* Lang, distal end of a zooecium showing complete calcification of the frontal membrane and operculum. *c*, *d*, *Rhammatopora gasteri* sp. nov. D. 40472, holotype, two normal zooecia showing apertural spine-bases.

Caudae generally long, narrow, tubular, widening distally into a wide, smooth gymnocyst which descends steeply, and is narrower laterally and distally to the aperture. The caudae of successive zooecia in a given series are increasingly long.

Zooecia narrowly rounded distally and tapering proximally into the caudae. Aperture longitudinally oval. Cryptocyst a narrow, descending, proximal shelf which may extend some way round the sides of the aperture. Opesia longitudinally oval, only slightly smaller than the aperture. Apertural rim slightly raised, with from 15 to 20, commonly 18, small apertural spine-bases. Regeneration is fairly common. Complete calcification of the frontal membrane and operculum occurs occasionally, as in D. 22905.

Heterozooecia, other than avicularia, are possibly occasionally present. In D. 2062, the lectotype, there is possibly one heterozooecium which is reminiscent, in its triangular form, of the kenozooecia of *Pyripora laxata* (d'Orbigny).

Avicularia and ovicells absent.

Measurements

Zooecia Lz = 0·70 to 2·33 mm. ho = 0·22 to 0·38 mm.
lz = 0·24 to 0·39 mm. lo = 0·15 to 0·17 mm.
ha = 0·27 to 0·45 mm. Lc = 0·15 to 1·95 mm.
la = 0·16 to 0·25 mm. lc = 0·03 to 0·08 mm.
Apertural ratio = 1·42 to 1·94.

Remarks. Lang (1915) separated Vine's specimens of *Membranipora gaultina* into two species. He placed those from the Red Chalk of Hunstanton, Norfolk (D. 2051–2, D. 20488–90), in *Rhammatopora vinei*, and retained, with a revised diagnosis, the specimens from the Gault of Cambridge as *R. gaultina* (Vine). He also introduced another new species, *R. pembrokiae*. According to Lang, the lateral gymnocyst of *R. gaultina* is 'small' and its aperture 'oval to ovate', whereas the lateral gymnocyst of *R. pembrokiae* is 'comparatively wide' and its aperture 'ovate to elliptical'. We have found, however, that the apertural ratios of Lang's specimens of *R. pembrokiae* are the same as those of *R. gaultina* and *R. vinei*. There is considerable variation in the width of the lateral gymnocyst in specimens which Lang assigned to *R. pembrokiae*, and in some zooecia the lateral gymnocyst is as narrow as in the lectotype of *R. gaultina* (Vine).

The distinction which Lang (1914*a*, p. 7, footnote) made between 'oval', 'ovate', and 'elliptical' apertures is not clear. Apertures which are more or less pointed, or which have almost parallel sides, or which are more nearly circular may be found in single zoaria assigned by Lang to *R. pembrokiae* and, as already mentioned, the apertural ratios are similar in the three species he recognized. Thus the characters used by Lang to distinguish the species are really not distinctive. Furthermore, the dimensions of *R. pembrokiae* and *R. gaultina* are similar and we consider the former to be a junior synonym of the latter.

The specimens from the Red Chalk, which Lang named *R. vinei*, are badly preserved, but, although it is not possible to identify all the diagnostic characters in any one zooecium, they can be distinguished in the zoaria as a whole. The dimensions of the species are similar to those of *R. gaultina*. Apertural spine-bases are occasionally preserved (e.g. in D. 2051 and D. 43483), but other pittings on the worn apertural margins may well be due to wear. Thus *R. vinei* is also synonymous with *R. gaultina*.

Stratigraphical distribution. Albian to Cenomanian, Chalk Marl.

Specimens. British Museum (Natural History): D. 2062—lectotype, see above. D. 22987, holotype, and D. 21729–34, D. 22880–907, D. 22986, D. 22988–3008, all paratypes, of *R. pembrokiae* Lang; zoarial fragments encrusting pieces of shell; Cenomanian, Chalk Marl, north-east of Cambridge; F. Möckler Collection. D. 2051, holotype, and D. 2052, D. 20488–90, all paratypes, of *R. vinei*, Lang; zoarial fragments encrusting pieces of *Inoceramus*; Red Chalk, Hunstanton, Norfolk; T. Jesson Collection. D. 43483—zoarial fragments encrusting *Inoceramus sp.*; Red Chalk, Hunstanton, Norfolk; J. E. Lee Collection. D. 43482—zoarial fragments encrusting *Inoceramus sp.*; Red Chalk, Speeton, Yorkshire; W. Bean Collection.

Rhammatopora gasteri sp.nov.

Plate 62, figs. 3, 4

Holotype. D. 40472. Zoarial fragment encrusting part of a valve of *Ostrea sp.* Cenomanian, upper part of zone of *Schloenbachia varians*. Pit south-west of Fox Inn, Southerham, Lewes, Sussex. C. T. A. Gaster Collection.

Diagnosis. Rhammatopora with aperture 0·16 to 0·27 mm. long, 0·08 to 0·17 mm. wide; apparently 10 to 13, commonly 12, apertural spine-bases.

Description. Zoarium encrusting; budding distal-median and uni- and bi-lateral commonly at right angles.

Caudae generally as long as, or longer than, the rest of the zooecia, narrow, tubular, and straight. In the holotype, the only available specimen, there are numerous short caudae, but these are near the beginning of individual series of zooecia in which successive caudae become increasingly longer: the longest measurable cauda is 1·17 mm. The caudae widen distally into a smooth, triangular gymnocyst which extends, much narrowed, round the aperture.

Zooecia distally rounded and tapering proximally into the caudae. Aperture longitudinally oval. Cryptocyst a narrow descending proximal shelf which, apparently, does not extend along the sides of the aperture. Opesia longitudinally oval, only slightly shorter than the aperture and of the same maximum width. Apertural rim slightly raised, apparently with from 10 to 13, commonly 12, very small apertural spine-bases. Complete calcification of the frontal membrane and operculum occurs occasionally. Regeneration of zooecia has not definitely been seen.

Heterozooecia, other than avicularia, have not been seen.

Avicularia and ovicells absent.

Measurements

Zooecia Lz = 0·45 to 1·53 mm.
lz = 0·15 to 0·27 mm.
ha = 0·16 to 0·27 mm.
la = 0·08 to 0·17 mm.
ho = 0·14 to 0·25 mm.
lo = 0·08 to 0·17 mm.
Lc = 0·23 to 1·17 mm.
lc = 0·03 to 0·05 mm.
Apertural ratio = 1·33 to 2·00.

Remarks. The holotype is the only specimen known to us. Although it is somewhat worn, the important details of most of the zooecia can be clearly determined without difficulty. Spine-bases occur on the apertural rims of some of the zooecia, are regularly spaced, and are exactly like those found in zooecia of similar size in other genera. Owing to wear, it is not possible to trace them all round an aperture, but in many zooecia they are so clear that they can be interpreted only as spine-bases.

R. gasteri sp. nov. differs from *R. gaultina* (Vine) in its smaller size and particularly in its fewer apertural spine-bases (cf. text-figs. 4*a–d*). The species is named after Mr. C. T. A. Gaster.

Stratigraphical distribution. Cenomanian, zone of *Schloenbachia varians.*

Specimen. D. 40472—holotype, see above.

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H. DIGHTON THOMAS
British Museum (Natural History),
London, S.W. 7
G. P. LARWOOD
Sedgwick Museum,
Cambridge

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THE PERMIAN LEIOPTERIID *MERISMOPTERIA* AND THE ORIGIN OF THE PTERIIDAE

by J. M. DICKINS

ABSTRACT. The musculature and dentition of *Merismopteria* Etheridge jun. 1892 are described and illustrated. Muscles are present both in front and behind the 'clavicle' or buttress ridge. Lateral and cardinal teeth may be present. *Merismopteria* is closely related to and may be a synonym of *Leiopteria* Hall 1883. Modern pteriids are considered to be derived from the Palaeozoic leiopteriids which lack a chondrophore and have a flattish ligament area with chevron-shaped or parallel-longitudinal ligament grooves and it is concluded that the 'pteriid' type of ligament with a chondrophore is independently developed in the pterioids and the pectinoids.

IN describing a specimen from the Bowen River, Queensland, Etheridge jun. (1892, p. 271) proposed a new generic name *Merismopteria*, designating as type *Pterinea macroptera* Morris (1845, p. 276, pl. 13, fig. 2; 3). The characters of this genus, including the nature of the clavicle and the anterior musculature, and the relationship to other genera, especially *Leiopteria* Hall, have caused considerable speculation.

Under the heading 'Generic Characters' Etheridge gave the following diagnosis:

> 'Pteronitiform in appearance, the anterior end lobe-like and well developed; posterior end alate. Area excavated along the cardinal edge of both valves, and deeply ridged for the reception of a ligament; cardinal teeth wanting but a strong clavicle descends in each valve before the anterior adductor muscles; one or more lateral teeth in each valve. Anterior muscle scars double and strong, the superior scar situated towards the umbones. External ornament of concentric ridges.'

Etheridge states under the heading 'Observations', however, that there is 'one lateral tooth only, either oblique or horizontal'.

In order to clarify the characters of *Merismopteria* an attempt has been made to find the type specimen or specimens described by Morris and according to Morris collected by Strzelecki from Spring Hill, Van Diemen's Land (Tasmania). According to a letter from the British Museum (Natural History) the types are not in this institution where most of the Strzelecki Collection is housed, so that it appears that they are lost. Two specimens, however, from the Strzelecki Collection (PL2865–6) are housed in the British Museum. These have the locality label 'Carboniferous Australia'. These and other specimens have been kindly lent by the British Museum, and, together with specimens in the Australian Museum, Sydney, and in the Bureau of Mineral Resources, Canberra, afford considerable additional information on *Merismopteria*.

Type Specimens of Pterinea macroptera *Morris*. Although Morris's figured specimen (or specimens) from Spring Hill, Tasmania, appear to be lost it is not proposed to choose a neotype at present.

Mr. M. R. Banks, of the Geology Department of the University of Tasmania, in a letter of 19 November 1958, says: 'I have so far been unable to find the Permian rocks at Spring Hill. . . . Permian rocks occur a few miles to the east at Eastern Marshes and about ten or fifteen miles to the west near Waddamana.' He also says the University of Tasmania has no specimens from this area. Although it is possible that PL2865 and

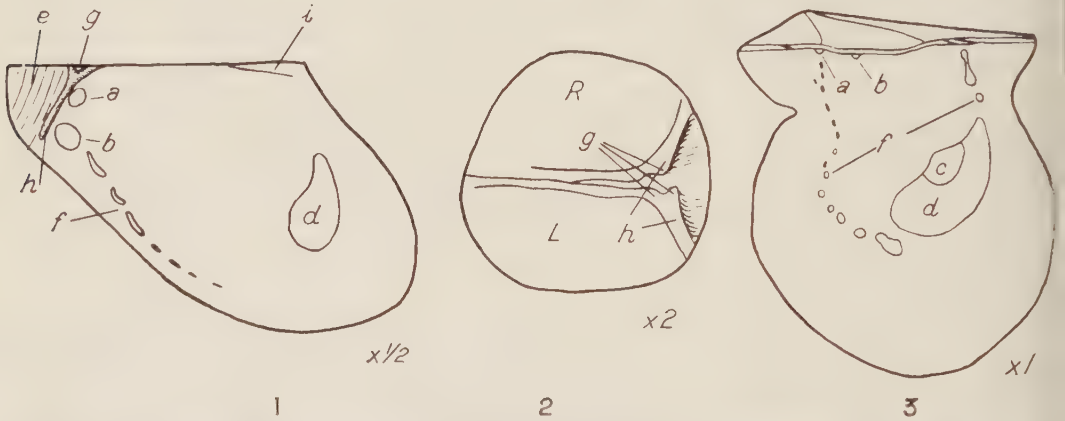
[Palaeontology, Vol. 3, Part 3, 1960, pp. 387–91.]

PL2866 are from the type locality it appears better to defer choice of a neotype until the locality of the specimens can be confirmed or until suitable topotype material is available.

PL2865 and PL2866 are contained in a light buff to white (? leached) dense silt to fine sandstone with many quartz grains, some mica, and, apparently, a clay matrix.

Dimensions of British Museum Specimens

Locality	*Number*		*Length*	*Height*	*Width*
Carboniferous Australia	PL2865 (internal impression)	Left valve	38	19+	2·5
		Right valve	36	21+	2·0
	PL2866 (internal impression)	Left valve	36	23	3·0
		Right valve	32	21	2·5
McCallum's Block, Bowen Coal Field, about 4 miles south-west of Collinsville, probably above Big *Strophalosia* Bed and below *Derbyia* Bed.	PL541 (internal impression)	Left valve	103+	63	18·0
		Right valve	103+	60+	16·0
	PL540 (external impression)	Right valve	46	31	6·0



TEXT-FIG. 1. Composite internal impression of a left valve of *Merismopteria*. 2, Cardinal teeth of *Merismopteria*. 3, Musculature of a right valve of *Pinctada vulgaris* (based on Newell 1938). *a*, *b*, *c*, impressions of pedal muscles; *d*, impression of 'posterior' adductor; *e*, impression of 'anterior' adductor; *f*, pallial line; *g*, cardinal teeth or their impressions; *h*, 'clavicle' (anterior buttress ridge) of its impression; *i*, posterior lateral tooth; *L*, left valve; *R*, right valve.

Musculature. Etheridge considered that the anterior muscle scar was situated behind the clavicle, an observation which I have been able to confirm (Dickins 1957, p. 30). On the other hand, in apparently closely related leiopteriids, for example *Dozierella* Newell (1940, p. 284), the anterior muscle is found in front of the 'clavicle' which thus represents a buttress ridge. The two specimens from the Strzelecki Collection allow a resolution of this apparent contradiction. Muscles are present both in front of and behind the 'clavicle'. In front of the 'clavicle' in PL2865 the presence of a relatively large anterior adductor muscle is indicated by muscle growth lines (the muscle track). The anterior adductor muscle is bounded behind by the 'clavicle' which is thus a buttress ridge confirming the interpretation made by Newell (1940, p. 283).

In PL2866, however, two distinct muscles occur behind the buttress. The larger, which is not much smaller than the anterior adductor, is situated immediately behind the buttress and lies below the smaller. The smaller is placed on the anterior side of the internal impression of the beak. Although they are unusually large, it seems likely that these muscles are connected with the action of the foot (pedal muscles).

Further information is given on the musculature by PL541, from McCallum's Block, Bowen Coal Field. The posterior adductor scar is large and kidney-shaped, situated over the posterior umbonal ridge. The intermittent pits of the pallial line run from the base of the ventral pedal muscle along the anterior side of the umbonal ridge towards the posterior adductor. A number of small round pits occur on the surface of the shell within the pallial line, marking the mantle attachment to the shell.

The musculature is thus more primitive than that characteristically found in adult living pteriids, the anterior adductor and the pedal muscles being considerably more highly developed.

Hinge structure. Examination of specimens in the Australian Museum, Sydney, and in the Bureau of Mineral Resources, Canberra, confirms Etheridge's description of the ligament (1892, p. 271) and shows this structure is of the same type as that described for *Leiopteria? carrandibbiensis* Dickins (1957, p. 30, pl. 4, figs. 13–17, text-fig. 4). A specimen from the collections at Canberra is figured. The ligament is borne on an area which is elongated on either side of the umbo, and on which are a number of parallel-longitudinal ligament grooves. Recognition of a posterior lateral by Morris, de Koninck, and Etheridge is confirmed by the presence of a lateral tooth in PL2866 and in specimens in the Australian Museum. In PL2866 a lateral tooth is visible in the left valve towards the rear of the cardinal margin. By analogy with living pteriids at least a single tooth could be expected in the right valve, although such a tooth has not been visible in most of the specimens which I have examined. However, even though the lateral dentition is difficult to see in internal impressions, because it diverges only slightly from the cardinal plate, it does appear possible that in some specimens or species lateral teeth are absent. Living pteriids vary in this way.

In PL2865 the impressions of small cardinal teeth are visible immediately in front of the umbos. In the right valve these comprise a projection with a groove on either side and in the left valve a socket for the projection of the right valve with a clasping lamella on either side fitting in the sockets of the right valve. These are similar to those of living Pteriidae and by analogy, like the lateral teeth, may be variable. The details of the dentition would appear to be of doubtful value for generic separation.

Shell structure. The main shell layer is composed of prisms at right angles to the surface (specimens in the Australian Museum). The prisms are of a similar size to those recorded for *L.? carrandibbiensis.* Under the hand lens the structure appears the same as that found in *Atomodesma.* It may be assumed that during life a thin inner nacreous layer was present.

Relationship to Leiopteria *Hall 1883.* Amongst described genera *Merismopteria* appears to be closest to *Leiopteria.* On the basis of Hall's diagnosis (1884, p. xiii) there is little to choose between the two, but the detailed characters of Hall's species still remain obscure and until more is known about these species it is not possible to decide whether

Merismopteria is a synonym of *Leiopteria* or not. Meantime perhaps *L.? carrandibbiensis* Dickins should be assigned to *Merismopteria* rather than *Leiopteria*. Such species as *Liopteria? dutoiti* Harrington (1955, p. 120, pl. 24, figs. 5, 11) and *Liopteria bonaerensis* Harrington (1955, p. 120, pl. 24, fig. 10) may be more closely related to *Merismopteria* than is suggested by their generic assignment to *Leiopteria*. (According to Neave (1939, p. 960) *Liopteria* is an emendment proposed by Fischer 1886 for *Leiopteria*.)

ORIGIN OF THE PTERIIDAE

In this paper the Pteriidae are restricted to those forms, characteristically with a well-developed prismatic shell layer, which possess the 'pteriid' type of hinge, that is with a single distinct ligament pit on the area. This does not include the Mesozoic forms such as *Meleagrinella*, *Oxytoma*, and *Maccoyella* which properly belong to the Pectinacea (see Ichikawa 1958). Pteriidae in this restricted sense are at least very rare in Palaeozoic rocks, and I know of no definite occurrence. However, *Bakevellia* King from the Upper Permian has multiple ligament pits on the area like *Perna* and is thus apparently derived from a form with a single ligament pit. Most of the Palaeozoic forms which have been referred to the Pteriidae have areas with a number of parallel-longitudinal or chevron-shaped ligament grooves and are more satisfactorily referred to the Leiopteriidae or other families.

Although *Merismopteria* differs in some important characters from modern Pteriidae, it shows sufficient similarity to suggest that the Pteriidae were derived from leiopteriids or related shells. The general shape and shell structure of *Merismopteria* are similar to modern pteriids, and its dentition and posterior musculature to species of *Pinctada*. In all these respects it is significantly different from the pectinoid forms. It differs markedly from the pteriids only in the anterior musculature, which is apparently more primitive and in the ligament structure. The poor development of the subauricular notch in right valves in Palaeozoic forms appears to be of lesser importance. From these data it seems that the 'pteriid' type of hinge was developed independently in the Pteriacea and the Pectinacea, a suggestion which has already been made by Newell (1942, p. 26). Alternative explanations such as derivation of the pteriids from the aviculopectinids seem unlikely. Such a derivation would require modification of the shell in a great number of respects, including shell shape, shell structure, and musculature to produce a type of shell already in existence but requiring essentially only modification of the hinge.

Bernard (1895–7) observed that the ligament was internal when it first appeared in the young pelecypod and concluded this was the primitive condition of nuculoids. Newell (1942, p. 28), after referring to Bernard's observation, states that 'in some genera such as *Pecten*, *Nucula*, *Pteria*, *Lima*, and *Ostrea*, this condition apparently continues to maturity'. Newell thus suggests the early internal ligament corresponds to the adult resilifer.

However, the phylogeny of at least some of these forms suggests that the early ligament recorded by Bernard is unlikely to be analogous with the adult resilifer, and indeed Bernard's ontogenetic studies also seem to show this. If Bernard's and Newell's suggestion were correct this would seem to contradict the conclusion that the 'pteriid' ligament is derived independently in the Pectinacea and the Pteriacea.

There seems little doubt, however, that the ancestors of the pteriids in the restricted sense are represented in the Upper Palaeozoic mainly by forms which have parallel-longitudinal or chevron-shaped grooves, and all these forms can be satisfactorily placed in the superfamily Pteriacea. Earlier in the Palaeozoic the superfamilies such as the Pteriacea, the Pectinacea, and the Mytilacea become less easy to distinguish as these groups converge but none of these earlier forms can be expected to possess the 'pteriid' type of ligament.

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J. M. DICKINS
Bureau of Mineral Resources, Geology and Geophysics,
Canberra, A.C.T.

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CHARACTERS AND RELATIONSHIPS OF THE MESOZOIC PELECYPOD *PSEUDAVICULA*

by J. M. DICKINS

ABSTRACT. The hinge structure and the musculature are described and illustrated. An anterior ear and a subauricular notch are present in right valves, the ligament is of the 'pteriid' type with a chrondophore, and the musculature is similar to that of *Chlamys*. The main shell layer is composed of concentric interlocking lamellae and the valves although inequal are biconvex. It is concluded that *Pseudavicula* is a pectinoid and appears to be most closely related to forms placed in the subfamily Streblochondriinae of the family Aviculopectinidae.

WHEN Etheridge jun. proposed the generic name *Pseudavicula* (1892, p. 449), with *Lucina anomala* Moore (1870, p. 251, pl. 14, fig. 4) as type, he gave the following diagnosis:

> 'Shell in general outline meleagriniform, but devoid of an anterior wing or ear. Valves compressed, closed, nacreous within, bi-convex, inequilateral. Cardinal margin thin, no area, or hinge teeth, but probably with a small ligament. Position wing moderately developed, but with little or no emargination. Adductor muscular scars subcentral, of medium size.'

The name *Pseudavicula* was apparently first published by Hudleston (1890, p. 244). It is clear from Hudleston's paper, however, that the name was derived from Etheridge's work and he states 'the diagnosis of *Pseudavicula* is not known to me'. He referred his specimens to *Pseudavicula anomala* (Moore) 1870 and placed *Avicula orbicularis* Hudleston 1884 in synonymy with *P. anomala*. Hudleston's use of the name thus does not effect the choice of type species.

In *Pseudavicula*, Etheridge placed two closely related species *Lucina anomala* Moore and *Lucina? australis* Moore (1870, p. 251, pl. 14, fig. 5). He also doubtfully referred *Avicula alata* Etheridge sen. (1872, p. 342, pl. 20, fig. 8) to this genus (p. 563). In 1907 he added, from Queensland, another species, *P. papyracea* Etheridge jun. (1907, p. 319).

In describing specimens from South Australia, Whitehouse (1925, pp. 27, 28) suggested that *P. australis* was a synonym of *P. anomala* and that the right valve of his specimens had no byssal sinus. He also showed that a 'pteriid' type of hinge was present (p. 28, pl. 1, figs. 2, 3) although this does not seem to have become widely known.

The three species, referred without doubt by Etheridge to *Pseudavicula*, form a distinctive closely related group in the Roma 'Formation' of Aptian age, and are widespread in Queensland, New South Wales, and South Australia, occurring sometimes in large numbers. *P. papyracea* has also been recorded by Glaessner (1945, p. 159, pl. 6, fig. 11; 1958, p. 201) from New Guinea, and I have found *P. papyracea* or a closely related species in the Canning Basin of Western Australia in deposits which are thus no doubt of Cretaceous age (Frezier Sandstone of Lindner and Drew: see McWhae, Playford, Lindner, Glenister, and Balme 1958, p. 108). The anterior ear and subauricular notch are also shown in right valves of these specimens.

The following features are revealed by a study of specimens in the collections of the

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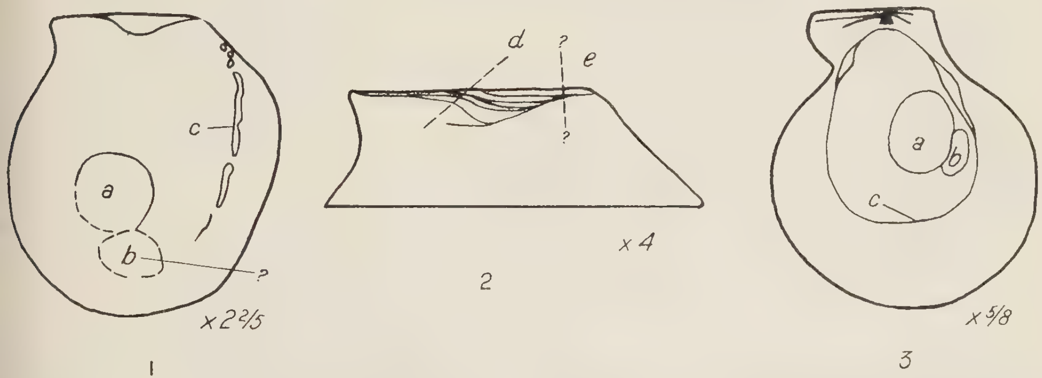
Geological Survey of Queensland and afford additional information on the character and relationship of the genus.

Structure of hinge and cardinal region. The characters of *Pseudavicula* are shown excellently in internal and external impressions from the south-west corner of Portion 53V, Parish of Bendemere, left bank of Yuelba (or Yuleba) Creek, Queensland. (Yuelba Creek is about 36 miles east of the township of Roma.) All the right valves appear to be smooth but the left valves apparently may be smooth or have delicate radial ribbing. A left valve showing radial ribbing is figured in the accompanying plate. According to Etheridge (1907, p. 326), *P. papyracea* is separable from *P. anomala* by the absence of radial ribbing so that, in this case, it is difficult to decide what species are present—apart from the radial ribbing the specimens do not appear to differ significantly.



TEXT-FIG. 1, Internal impression of a right valve of *Pseudavicula*. 2, Impression of ligament of *Pseudavicula*. 3, Musculature of a right valve of *Chlamys islandicus* (based on Newell 1938). *a*, *b*, adductor impressions; *c*, pallial line; *d*, line of posterior edge of chondrophore; *e*, line of anterior edge of chondrophore.

The umbo is almost but not quite terminal, and a small anterior ear is visible in several right valves, one of which is figured. The anterior ear is relatively very small and would easily be lost by abrasion before burial or by erosion or breakage during weathering or during breaking out from the rock. This no doubt explains why the ear has not previously been recorded. The ear is separated below from the rest of the shell by a small but distinct subauricular notch (the term 'subauricular notch', used by Cox 1943, p. 153, is preferred to the perhaps misleading term 'byssal notch'). Except in distorted specimens the anterior ear is in the same general line as the rest of the cardinal margin.

The structure of the ligament is of the 'pteriid' type, characteristic of the aviculopectinids and the living pteriids. The ligament is lodged on a flattish ligament area; behind the umbo the area thickens and deepens to form a chondrophore or resilium pit. The chondrophore is marked off at the back by a distinct but rounded oblique boundary, the upper part of which points to the front. The anterior boundary is not clear in any of the specimens but appears to be more upright than the posterior boundary and situated level with the umbo. The area has parallel-longitudinal growth-lines and acks any longitudinal ligament grooves. The structure is different from that found in

Deltopecten, where no chondrophore boundary is present, and is distinct from the leiopteriids where distinct longitudinal or chevron-shaped ligament grooves are present.

Musculature. The musculature of the right valve is shown in the accompanying text-figure, where a right valve of *Chlamys* is also illustrated. The right valve of *Pinctada* has been figured in the preceding paper on *Merismopteria*. An important feature of *Pseudavicula* is the closer resemblance to *Chlamys* than to *Pinctada*: that is, it is more closely related to the Pectinacea than to the Pteriacea.

Convexity of valves and shell structure. Etheridge (1907, p. 319) discussed the question of relative convexity of the right and left valve and concluded that in all three species, the left valve is more convex and the umbo higher than in the right. An examination of the collections in the Geological Survey of Queensland confirms Etheridge's conclusion. Although both valves are convex, in all specimens examined the left valve was more convex than the right. The inequality, however, varies considerably.

The specimen figured by Etheridge (1892, pl. 21, fig. 14) which was later the only specimen referred by him to *Pseudavicula papyracea* (1907, p. 319), and which must thus become the holotype, is preserved in the Geological Survey of Queensland. The specimen is exfoliated but shows a layer of concentric interlocking lamellae, such as Newell (1938) has shown to occur in *Aviculopecten* and Ichikawa (1958) has recently shown to occur in *Meleagrinella* and *Oxytoma*. The specimen figured by Etheridge (1892, pl. 21, fig. 16), which in my opinion is also referable to *P. papyracea*, also shows concentric interlocking lamellae, which are just visible to the naked eye.

Relationships of Pseudavicula. The small anterior ear and especially the subauricula notch in *Pseudavicula*, together with other characters, suggest derivation from member either of the Pectinacea or the Pteriacea in which the anterior ear and subauricula notch were more strongly developed. In considering whether *Pseudavicula* belongs to the Pectinacea or to the Pteriacea, the musculature and the shell structure are of significance as the type of hinge present occurs in both superfamilies. Each definitely indicates relationship to the Pectinacea. The muscle pattern is of the 'pectinoid' type; the shell

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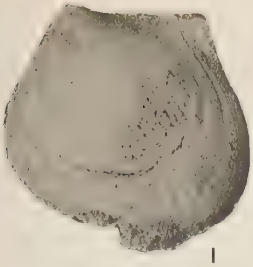
EXPLANATION OF PLATE 63

Figs. 1–5. *Pseudavicula* cf. *papyracea* Etheridge jun. 1907. Specimens from south-west corner of Portion 53V Parish of Bendemere, left bank of Yuelba Creek, about 36 miles east of Roma. The numbers are those of the Geological Survey of Queensland. 1, Latex impression of a left valve, ×2. No. F. 2317. 2, Latex impression of right valve showing anterior ear, ×2, No. F. 2316, dorso-lateral view. 3, Same, lateral view, ×2. 4, Internal impression of dorsal part of a right valve, ×4, No. F. 2315. 5, Complete view of same shell, ×2.

Figs. 6–12. *Merismopteria sp.* All specimens are from rocks of Permian age. 6–8, British Museum (Natural History) No. PL2865, 'Carboniferous', Australia. 6, Plasticene impression to show cardinal teeth, ×2. 7, Normal view, ×1. 8, Specimen tilted up at front to show muscle growth-lines, ×2. 9–10, British Museum (Natural History) No. PL2866, 'Carboniferous', Australia. 9, Normal view, ×1. 10, Dorsal view of right valve, ×1. 11, British Museum (Natural History) No. PL541, McCallum's Block, Bowen Coal Field, lateral view of left valve, ×½. 12, Commonwealth Palaeontological Collection Type No. 107, Field No. JB35, east end of Steamer's Beach, Jervis Bay, New South Wales, from beds probably equivalent to the Conjola Beds of David and Stonier. Internal impression of right valve showing longitudinal ligament grooves and a posterior lateral tooth, ×2; the front part of the shell is missing.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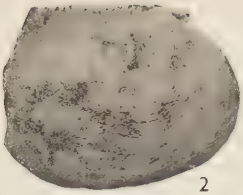
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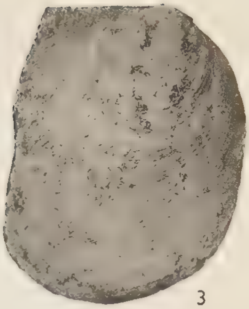
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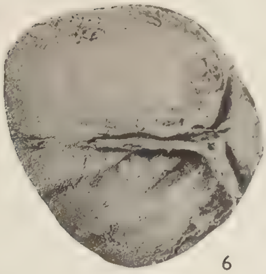
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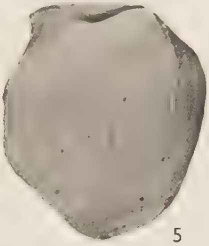
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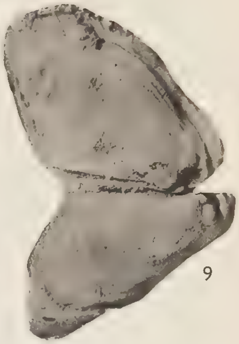
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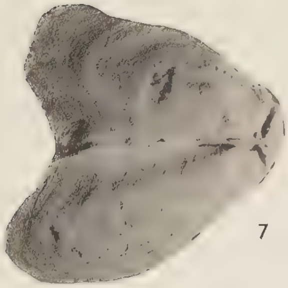
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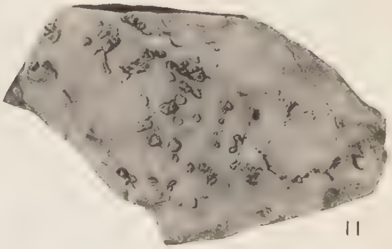
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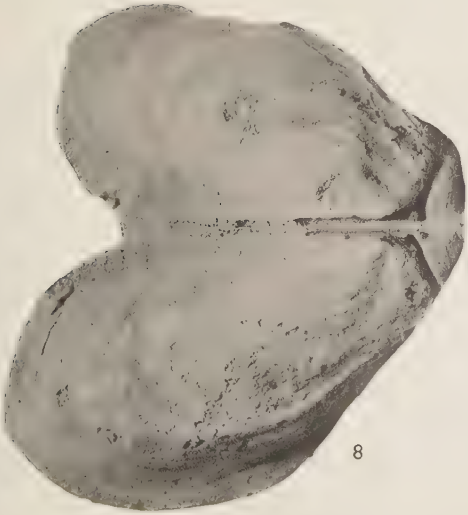
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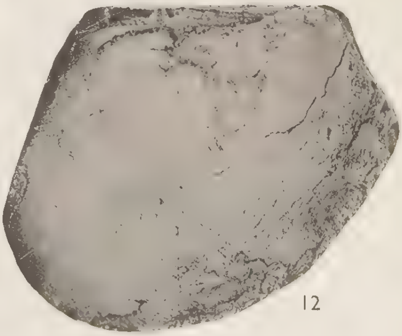
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DICKINS, Australian Pelecypods

tructure is characteristic of that found in the aviculopectinids and distinctly different rom that found in the pterioids where, characteristically, a prominent prismatic layer is leveloped in each valve and the lamellar structure is absent. In the Upper Palaeozoic the iconvex Streblochondriinae of Newell (1938) appear likely to be ancestral to *Pseuda- icula.*

In the Jurassic the biconvex *Pseudomonotis laevis* (Blake and Hudleston) Arkell (1931, . 200, pl. 24, figs. 11, 11*a*, 12) appears to be closely related to *Pseudavicula* and may ven be referable to this genus. In the Cretaceous *Pseudomonotis superstes* Spitz (1914, . 201, pl. 18, figs. 6, 7) from the Gieumal Sandstone of the Himalayas appears to be loser to *Meleagrinella* Whitfield 1885 than to *Pseudavicula* unless two species are present mong Spitz's specimens.

onclusion. The present evidence supports a previous suggestion, based on a study of ermian forms, that a number of Mesozoic genera which have usually been placed by revious authors in the Pteriidae are descended from the aviculopectinids (Dickins 1957, . 44). Ichikawa (1958) has independently arrived at a similar conclusion, which he sup- orts with ample and convincing evidence. Ichikawa (1958, p. 193) also agrees with ewell (1938) in considering the Aviculopectinidae are better placed with the pectinoids han with the pterioids. The author has discussed evidence in the immediately preceding aper which suggests that by the end of the Carboniferous period the Pectinacea and he Pteriacea were already distinct groups, evolving separately, and thus would place he Aviculopectinidae and derived forms in the superfamily Pectinacea and separate hem from forms placed in the Pteriacea.

It can be concluded that *Pseudavicula* is derived from aviculopectinid forms and is ossibly close to forms placed by Newell in the subfamily Streblochondriinae.

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J. M. DICKINS
Geological Section,
Bureau of Mineral Resources, Geology and Geophysics,
Canberra, A.C.T.

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